GROWTH AND DEVELOPMENT OF SCOTTISH BLACKFACE AND ICELANDIC SHEEP

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I hereby declare that this thesis has been composed by myself and that all the work reported is my own.

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ABSTRACT OF THESIS

Two studies of growth and development in sheep were undertaken, one at Edinburgh, the other in Iceland, between 1977 and 1979. The main objectives were twofold: (1) to examine the 'normal' pattern of growth and development, in relation to presently acknowledged growth principles; and (2) to evaluate genetic and sexual influences, with special emphasis on the effects of conformation on growth and carcass characteristics.

Two breeds of sheep were involved; at Edinburgh, the Scottish Blackface, and in Iceland, the Iceland sheep. Common to both experiments was the comparison of different genotypes of the same breed, distinct in external body form. These had been created by continuous selection, over 20 - 25 years, the sole criterion in Edinburgh being live weight corrected cannon bone length, while in Iceland, other criteria of conformation were included in addition to cannon bone length. Both experiments involved the serial slaughter and full anatomical dissection of lambs from the time of birth to weights approaching maturity. At Edinburgh, controlled individual feeding was involved after weaning, whereas in Iceland, most lambs were slaughtered off pasture.

The data have been analysed in several different ways, including, for relative growth, the use of Huxley's allometric equation, the computation of relative weight increases, based on the weight at birth, and the comparison of percentage proportions at different weights or ages.

Significant differential growth patterns were demonstrated at all levels of the anatomy. Frequent changes in these made the application of Huxley's formula unsafe over extended periods of growth. The developmental orders of the various body organs, parts or tissues were, in the main, consistent with present ideas. However, some questions were raised, particularly regarding certain aspects of skeletal and muscular development, and these are discussed in light of the present findings.

Sexual differences were clearly apparent, both in absolute and relative terms. The males grew faster than the females and were later maturing, as indicated particularly by delayed fat deposition. With respect to carcass proportions, masculinity was expressed in superior development of the neck and thorax arising from all constituent tissues. By contrast, the females were better developed in the hind quarter, which gave them an advantage in muscle weight distribution over the normal range in slaughter age.

While genotype differences in live weight gain and feed conversion efficiency were inconclusive, significant effects were demonstrated on the relative development of the different body parts and tissues at any given age or weight. In Iceland, the selection for a short cannon bone and compact body form had grossly reduced skeletal weight, increased muscular thickness, the muscle: bone ratio and the proportion of back muscles, at the cost of neck and thorax muscles, and brought forward fat deposition, resulting in earlier attainment of marketable condition. The Edinburgh selection was less effective in altering carcass shape or composition, due to the break-down of intraskeletal proportions, the greatest selection effects being exerted on the lower limb bones and gradually diminishing in approaching the body trunk. The practical implications of these findings are discussed, and it is concluded, that breeding can effectively alter the animal's constitution, both as regards the tissue composition and the area to area distribution of the carcass.

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CHAPTER 1.

GENERAL INTRODUCTION

The concept of growth and development plays a fundamental role in the production of meat animals for at least three important reasons. (1) The course of growth may influence the subsequent performance of breeding stock; (2) the rate and efficiency of growth of the young to a marketable condition are two major determinants of commercial success; and (3) the value of the final product, the carcass, is largely governed by certain qualities associated with the state of development at slaughter.

Numerous definitions of growth are to be found in the literature, varying greatly in their complexity, depending on which aspects of the growing process have been under consideration. In the present thesis, the definition by Hammond (1952) has been adopted, i.e. that 'as an animal grows up two things happen: (1) It increases in weight until mature size is reached; this we shall call Growth, and (2) it changes in its body conformation and shape, and its various functions and faculties come into full being; this we shall call Development'.

There is no one universal definition of an ideal meat carcass, and it is a major challenge to the animal producer to meet with the ever changing demands of the general public. However, the common feature to all markets is that the carcass should contain a minimum of inedible or 'waste' tissue. In general terms, the increasing demand is for lean meat associated with an optimal amount of fat, commensurate with the respective consumer. Furthermore, certain carcass joints normally fetch higher prices than others, the loin and hind leg being of greatest value, while the flank, breast, shank and neck are the cheapest joints. An ideal meat animal can therefore be described as one with a high ratio of muscle to bone and a high proportion of the most valuable joints, while possessing the ability to be within acceptable limits of fatness at the most economic time of slaughter.

While, for centuries, producers in Great Britain (and later in other countries) have sought to improve their livestock for meat characteristics, it is only over the last five to six decades that scientists have involved themselves in developmental studies concerned with the qualitative aspects of meat production. Probably the most outstanding contribution in this field, is that of the Cambridge school, whose work was initiated by Sir John Hammond and subsequently continued by his students

(see Pålsson, 1955). These workers were concerned with combining the skills of the geneticist, anatomist and nutritionist to be successfully incorporated into the technology of animal production.

Their comprehensive anatomic approach to the study of growth and development resulted in the elucidation of several fundamental growth principles relating to normal growth, as well as to the possibility of manipulating the developmental patterns by genetic and nutritional means.

The practical implications of these findings were seen by the original workers as follows: (1) Since the different body parts and tissues were found to grow at different rates and thus change in their relative proportions with age, there has to be an optimal stage of development for slaughter. (2) Because of differential nutritional effects on the various body components, it should be possible to modify the animal's conformation and composition by controlling the level of nutrition. (3) Livestock could be genetically improved by selecting either directly for desirable meat qualities in the breeding flock, or indirectly through easily measured characteristics associated with such qualities. Concerning the last aspect, both Hammond (1932) and Pålsson (1939, 1940) highlighted the form of the skeletal frame as a key to the improvement of meat producing animals.

Various aspects of the Cambridge theories have met with criticism in recent years, the major areas of dispute concerning the extent to which the constitution of an animal can be genetically or nutritionally manipulated. Much of the controversy has arisen through different approaches to the analysis of growth data, such as, for instance, the choice of an independent variate, with which to compare relative changes in the body (Elsley, McDonald and Fowler, 1964). Furthermore, whereas the Cambridge school, in general, expressed their results as ratios of one part to another, to the whole, or to the same part at an earlier age, and described the development in terms of changes in these proportions, Tulloh (1963) argued that Huxley's (1932) allometric equation provided better means of describing such growth phenomena as were being studied. The allometric theory (see Chapter 2.10.) assumes a constant ratio of the specific growth rate of an organ or part to that of the whole body, regardless of environmental influences, and is thus in direct conflict with the concept of differential nutritional effects on developmental patterns. While vast research has been conducted into this particular aspect of growth and development over the last two decades, the

subject is still open for debate. Similarly, the potential for genetically improving the meat producing qualities of livestock is currently disputed. Contrary to the Cambridge school ideas, there are those who maintain that the distribution of bone and muscle within the carcass are two relatively inflexible characteristics, over which the breeder can not have but limited control, and some have gone as far as arguing that any attempts to alter the proportions of muscle, in the different carcass regions, are a complete waste of time (Berg and Butterfield, 1976).

The basic objectives of the present study were twofold: Firstly, to examine the 'normal' process of growth and development in sheep, in relation to presently acknowledged principles of growth and the merits of some of the different methods of expressing developmental changes. Secondly, to evaluate genetic and sexual influences on growth patterns and important carcass characteristics, with particular emphasis on the question: Does conformation have a role in the improvement of meat producing animals?

CHAPTER 2.

MATERIALS AND METHODS

The two experiments, to be described, were undertaken between 1977 and 1979, one at Edinburgh the other in Iceland. While many features were common to both experiments and will be described simultaneously, there were certain outstanding differences, in particular, in the experimental design and the different breeds of sheep used for each trial. Both trials, however, involved the serial slaughter of animals at different stages of maturity and the complete physical dissection of carcasses. By contrast, most of the Icelandic lambs were slaughtered from pasture, whereas controlled individual feeding was a major feature of the Edinburgh trial.

2.1. EXPERIMENTAL ANIMALS

a) The ABRO-selection lines.

In 1955 The Animal Breeding Research Organization (ABRO) initiated a long-term selection programme within their flock of Scottish Blackface sheep. By continuous two-way selection for cannon bone length, three selection lines, long (L) short (S) and control (C) were established, the C-line being unaffected by artificial selection. The objectives, selection methods and production features associated with this programme have been described in detail by Purser (1956, 1973, 1980).

Since the intention in these studies was to alter skeletal dimensions and thus the shape of the sheep, but without affecting body weight, a weighted selection procedure was used, ie. 'corrected cannon bone length' = (cannon bone length (cm) - 0.17) × (body weight (kg) - 14). Selection was based on measurements recorded at eight weeks of age. The body weight adjustment , however, was not completely successful, as L-ewes were on average 4 - 5 % heavier than S-ewes after 15 years of selection. Table 2.1.1. shows the mean cannon bone lengths and body weights of ewe hoggs born 1969 - 1973 as well as the weights of ewes pre-mating from 1970 - 1973 (from Purser, 1973).

Table 2.1.1. Mean cannon bone lengths (mm) and body weights (kg) of breeding ewes (ABRO-lines).

Line	Cannon bone length at 14 mths.(mm)	Body weight (kg) Ewe hoggs	Ewes
Long	137.4	30.6	43.1
Control	125.4	29.4	42.3
Short	111.9	29.0	41.1

These three selection lines provided the lambs for the Edinburgh study, all of which were born in late April - early May, 1977.

b) Icelandic sheep.

Icelandic sheep belong to the North European short-tailed race of sheep. For centuries the sheep were kept primarily for milk production; it was not until the 1930's that any systematic work began to improve the breed for fat lamb production. A major objective in the breeding work since, has been to improve carcass conformation. Even so, the average Icelandic sheep is still relatively poor in conformation, compared with traditional British mutton breeds. (For further information on the structure of the Icelandic sheep industry, see Pálsson, 1965).

Sheep breeding work has been carried out by the Icelandic Agricultural Research Institute since 1951, at the Hestur experimental farm. Within the greatest part of the flock, selection has been exercised using three main criteria: short cannon bone and 'fleshiness', high growth rates and fecundity. The primary aim has been to improve conformation and short cannon bone length has been the dominating single feature in the selection programme. However, considerable attention has also been paid to the thickness of the loin and the 'fullness' of the leg. Concurrent with the main programme, a small nucleus flock has also been kept within which selection has been for a long cannon bone; the other criteria having remained the same.

In the autumn of 1976, 27 short cannon bone ewe lambs were selected from the main flock. In addition, seven ewe lambs were also selected from the long-cannon nucleus and another 20 purchased from three neighbouring farms. The breeding policy on these farms was known to be aimed exclusively at high production, with no attention being paid to conformation. Furthermore, there were known to be blood-links between the sheep on two of these farms and the homeflock. These ewe-lambs were chosen to be as long-legged as possible, but of similar weights and ages as the

27 lambs from the short-legged flock.

The two flocks, each of 27 lambs, were kept at Hestur to provide the lambs for the present growth and carcass study. All the rams used were from the L- and S-nuclei of the homeflock for the L- and S-flocks, respectively. Table 2.1.2. shows the mean weights and cannon bone lengths of the two flocks at weaning and at 28 months of age.

Table 2.1.2. Cannon bone lengths and body weights of breeding ewes (Iceland).

Type	Cannon bone length (mm)		Body weight (kg)	
	Age: 4 mths.	Age: 28 mths.	Age: 4 mths.	Age: 28 mths.
Long	125.0 ± 0.41	135.4 ± 0.78	38.6 ± 0.71	56.7 ± 0.93
Short	109.9 ± 0.79	119.4 ± 0.62	39.1 ± 0.77	58.7 ± 0.90

2.2. MANAGEMENT OF BREEDING FLOCKS

a) Edinburgh.

During the year, prior to the experiment, the ewes were wintered outside with only minimal supplementary feeding. At mating time, they were brought into low-ground paddocks, in groups, each group having been allocated to a ram of the same genotype. Lambing took place in late April - early May. The ewes were then kept in closed fields and attended once a day for feeding as well as eartagging, weighing and recording all new-born lambs. During this period the ewes were fed small amounts of hay and given free access to concentrate blocks. After lambing, the whole flock was returned to the hill and were herded in a traditional fashion.

b) Iceland.

The two breeding flocks, each of 27 ewes, were kept under identical conditions of housing, feeding and grazing throughout the experimental period. In winter they were kept apart in the same house and fed identical rations. All ewes were oestrus synchronized, using 'progestagen' sponges, to minimize the variation in lamb ages. Ewes, that returned to heat, were mated again, but their lambs were excluded from further study, except for a few, which were killed at birth. Lambing took place, inside, in mid-May. The lambs were weighed, eartagged and recorded within 24 hours of birth. The separation of the two flocks continued for three to four weeks after lambing, during which time feeding was maintained outside. Thereafter the

flocks were grazed together in an enclosed area, of largely uncultivated moorland, until weaning at the end of August, when the lambs were 16 weeks old.

This same standard procedure was maintained over the three years to produce the lambs used in the present study.

2.3. SUMMER MANAGEMENT OF LAMBS

a) Edinburgh.

As previously stated, the breeding flocks, with lambs, were returned to the hills after lambing time. The sheep were then gathered again at the end of June, when the lambs were, on average, eight weeks old. At this time the lambs were weighed, their cannon bone length measured and all male lambs were castrated. Only castrated males were used for subsequent study and the greatest number of these lambs were born and reared as singles.

In preparation for the feeding trial, ewes and lambs were allocated to 'aftermath' grazing at the end of July, when both lambs and ewes had free access to a complete concentrate diet until weaning in late August; the aim being to get the lambs used to the diet and thus reduce the usual growth check at weaning.

After weaning, 122 lambs were transferred from the ABRO-farm to the School of Agriculture farm, where facilities were available for individual feeding. The lambs were initially penned in groups of four and given free access to hay and water. The experimental, barley-based, diet was introduced in small amounts at first, but gradually increased to ad lib. levels over a period of three weeks, after which the feeding trial commenced.

b) Iceland.

All lambs followed their dams over summer and were weaned at the end of August, when 16 weeks old. Thereafter they were grazed together on rape and grass for eight weeks, apart from 12 lambs in 1978, which were individually fed a standard ration to slaughter at 24 weeks. Live weights were recorded, at regular three weekly intervals, from birth to weaning and subsequently every four weeks.

2.4. EXPERIMENTAL DESIGN

a) Edinburgh.

The major part of the study at Edinburgh was concerned with post-weaning growth and development of the three previously described genotypes and the effects of moderately different levels of nutrition.

Three planes of feeding were involved, High (H), Medium (M) and Low (L), with slaughter involving groups of eight lambs at four predetermined live weights. An initial group of eight lambs were killed at the onset of the trial, as well as two groups at earlier ages. The first group of 12 lambs (2 males and 2 females from each line) were killed at birth and a second group of eight wether lambs at an average age of 12 weeks. A further group of nine lambs were to be continued on high plane feeding to live weights close to maturity.

Fewer S-lambs were available than either C- or L-lambs, which resulted in two S-lambs being allocated to each group with three C- or L-lambs; hence the groups of eight. Furthermore, a total of 16 lambs either died or had to be killed prematurely because of ill health after the beginning of the feeding trial. The inevitable result of these losses was a reduced number of lambs in many slaughter groups, and in some cases it was necessary to transfer lambs between groups (within planes of nutrition). Thus, the final plan fell somewhat short of the initial design.

Table 2.4.1. Experimental design (Edinburgh).

Pre-trial slaughter groups				Plane	Line	Designated Group mean weight at slaughter (kg)				
Line	Birth	12 wks. (17kg)	19 wks.+ (20kg)			30	35	41	46	Mat.(83)
L	4	3	3		L	3	3	3(2)	3(2)	3
C	4	3	3	High	C	3	3(2)	3(2)	3	3
S	4	2	2	(ad lib)	S	2	2	2	2	3(1)
					L	3(2)	3	3(2)	3	
				Med	C	3	3	3	3	
				90% ad lib	S	2	2	2(1)	2(1)	
					L	3(2)	3(2)	3(2)	3	
				Low	C	3	3	3	3	
				75% ad lib	S	2	2(1)	2	2	

+) Initial group to the feeding trial.
Values in parenthesis indicate actual numbers slaughtered.

The allocation of lambs to treatments and slaughter groups was undertaken by weight-restricted random sampling. Pre-trial weights were used to divide the Long and Control lambs into three, and Short into two, equally large weight classes. Fourteen groups of eight lambs were then formed by selecting at random, one lamb from each weight class, for each line. These 14 groups were randomly pre-allocated to one of the four slaughter groups within each plane, as well as initial slaughter and the maturity group, to which one S-lamb was later added.

All lambs in any one slaughter group were killed on the same day, when the mean weight of that group had reached the target weight.

b) Iceland.

The experiment in Iceland, contrary to that in Edinburgh, was not designed to systematically study nutritional effects. The emphasis was purely on the comparison of the growth and carcass characteristics of two contrasting genotypes. Nevertheless, the design did allow for the study of sexual differences and, to some extent, permitted the influence of type of birth and rearing on growth and carcass characteristics to be quantified.

Equal numbers of males and females were used and these were either singles or twins. No triplets or twins, reared as singles, were included in the analysis and all lambs, showing signs of illness for any length of time, were excluded.

In this trial, all animals were slaughtered at fixed ages. All were born within a time span of five days, each year, allowing whole groups to be killed on the same day with only minor variations in age. The first group was killed at birth and subsequent six groups at 6, 16, 20, 24, 48 and 74 weeks of age, respectively. The distribution of lambs, from each type and sex, over the experimental period, is summarized in table 2.4.2.

Table 2.4.2. Experimental design (Iceland).

		AGE AT SLAUGHTER						
Type/sex		Birth	6 wks.	16 wks.	20 wks.	24 wks.	48 wks.	74 wks.
LONG	M	2	2	4	4	4	2	2
	F	2	2	4	4	4	2	2
SHORT	M	2	2	4	4	4	2	2
	F	2	2	4	4	4	2	2

From birth to 24 weeks, there was one single per sub-group, ie. four in each slaughter group, while all lambs in the 48 and 74 weeks slaughter groups were singles, born from hoggs in 1977, but resembled the twins in subsequent years with respect to birth weight and pre-weaning growth. They were grazed together for six weeks after weaning and subsequently fed on hay and concentrates over winter. Eight of these lambs were killed at 48 weeks in April 1978, the remaining 12 being grazed together over summer and killed in October at 74 weeks of age.

The disproportionate number of lambs allocated to the 16, 20 and 24 weeks slaughter groups, reflects the special interest in Iceland in carcass development over this age interval.

The selection of lambs for slaughter, at each stage, was carried out by weight-restricted random sampling.

2.5. FEEDING TRIAL MANAGEMENT (Edinburgh)

The lambs from the three genotypes were offered three planes of nutrition, High (H), Medium (M) and Low (L). The H-plane lambs were fed ad libitum, daily allowances being approximately 10% in excess of intake. The M- and L-planes were set as 90% and 75% of H-plane feeding and were predicted to support growth rates of 85% and 70% of those of the H-plane lambs, respectively. The restricted levels were adjusted according to mean live weights of the lambs on each plane, rather than for individual lamb weights. Thus, the M- and L-plane lambs always received 90% and 75% of ad lib. intakes of equally heavy lambs on the H-plane, respectively. Live weights were recorded every two weeks and the levels of feeding revised after each weighing.

During the trial, each lamb was individually penned on straw bedding with access to fresh water at all times. Feeding was undertaken once daily. The diet offered was a pelleted compound of whole barley and protein + mineral mixture, which was weighed out in individual daily rations according to feeding plane. Each lamb was also given approximately 20 g of hay every day. Feed refusals were weighed three times a week, and cumulated individual weekly refusals were sampled for dry matter determination.

As well as chemically analysing the diet, two separate balance trials were undertaken to determine its metabolizable energy value (ME)

and digestible crude protein (DCP) content. The full details and discussion of the diet evaluation are presented in Appendix 1.

2.6. SLAUGHTER AND DRESSING PROCEDURE

In both trials, live weight at slaughter was taken as the mean of two weighings, on the day before and on the actual day of slaughter.

Apart from the birth group, all lambs in Iceland were transported 20 km by road to the abbatoir and slaughter commenced 1 hr after arrival. In Edinburgh, slaughtering was undertaken at the School of Agriculture Carcass Evaluation unit, 2 km from the farm.

The lambs at birth were killed by intracardiac injection of 5 ml $MgSO_4$ in Edinburgh, and not bled, whereas in Iceland the throat was cut and the spinal cord severed. All other lambs were stunned by a cap and bolt pistol, followed by bleeding, in Edinburgh, but anesthetized and subsequently bled, in Iceland. During the dressing, various offal parts (see Appendix 2 for details) were removed, cleaned and weighed to the nearest 0.01 - 1.0 g,depending on the weight of the part. Following slaughter, the whole carcasses were weighed, sealed in polythene bags (in Iceland only), frozen at -20°C and stored for 6 - 15 months.

2.7. CARCASS MEASUREMENTS

Six external carcass measurements, relating to development, were recorded prior to jointing and five further measurements as jointing progressed. On completion of the dissection, 43 measurements were also recorded of bone dimensions.

The carcass measurements recorded were those of Pálsson (1939) and are described in detail, together with the bone measurements in Appendix 3.

2.8. CARCASS JOINTING AND DISSECTION

Prior to dissection, each carcass was allowed sufficient time to thaw at 5 - 10°C and was covered with moist clothing to minimize moisture loss. Similar care was taken with all carcass parts throughout the dissection process.

The jointing and dissection method employed in the Edinburgh trial was largely based on the technique developed by Jackson at the Edinburgh School of Agriculture, which has been described in detail by Weddell

(1973). However, as skeletal development was an important attribute in this study, the original jointing procedure was modified to prevent damage to the bones. Thus, carcasses were split by removing the right side flesh from the central skeletal structures, leaving the intact vertebral column, pelvis and sternum with the left side. Using the left side, the four major retail cuts, gigot, loin, rib and shoulder, were separated at Jackson's 'anatomical check points'.

The dissection of each joint involved the separation, cleaning and weighing of subcutaneous fat, intermuscular fat, muscle, bone and 'waste tissues'. The degree, to which individual muscles and bones were recorded separately, varied according to trial. The methods employed in jointing and dissection are described in detail in Appendix 4.

In Iceland, the Edinburgh jointing technique was used in combination with the individual muscle technique, described by Fourie (1962, 1965).

2.9. DISSECTION OF THE HEAD AND FEET

The head and feet were allowed to thaw overnight at 5 - 10°C prior to dissection. In the Edinburgh trial, the lower mandibles were dissected out of the head and the metacarpal and metatarsal bones (cannons) from the left feet. In Iceland this dissection involved the cleaning of all bones in the head and left feet, as well as the separation of other components. The methods employed are described in Appendix 5.

2.10. STATISTICAL ANALYSIS

A number of statistical methods have been applied to the data. All major calculations have been carried out by the use of Harvey's (1977) 'Mixed Model Least Squares and Maximum Likelihood Computer Program'. Mainly, the analysis involved the fitting of least - squares constants for:

1) Main effects - e.g. Genotype, Sex, Type of birth.
2) Two-factor interactions between main effects.
3) Pooled partial regressions for continuous independent variables (linear or linear and quadratic) - e.g. Age or Time on trial, carcass wt. etc.
4) Interactions between main effects and independent variables (i.e. the computation and testing of separate regressions for each class within a main effect).

The general approach to any analysis was to include in the

initial model all variables, discrete or continuous, which could be defined and were considered to be of biological significance to the current problem. Such variables were gradually eliminated until only those remained, which showed significant effect ($p < 0.05$) on one or more of the dependent traits that were being studied. The finally chosen models are illustrated, for a number of traits, by tables of variance analysis in Appendix 6. The presentation of such tables for all the traits studied would be too voluminous.

Live weight gains were studied in terms of:

1) Mean weights at fixed times.
2) Average daily gains between fixed times.
3) Regressions of live weight on age or time on trial.

In case of the Edinburgh feeding trial, the analyses were done, either within feeding planes, or by including average daily D.M. intake as a partial covariate.

Similar methods were used to estimate changes in carcass or tissue weights over defined periods prior to slaughter. Initial weights were then estimated by log-log regressions based on the appropriate slaughter groups. It is acknowledged that such estimations can never be precise, however, the smaller the initial weight is, relative to the final weight, the less important the errors will be.

Relative growth rates of body parts, organs or tissues have been studied in one or both of two ways. Firstly, by calculating the multiplication of the weight of an organ, part or tissue over a specified time interval, using unadjusted group means. Secondly, by the use of Huxley's (1932) allometric equation:

$$y = ax^b$$

which was generally used in its logarithmic form:

$$\log y = \log a + b \log x.$$

Differentiation of the logarithmic form, with the inclusion of time (t), yields the equation:

$$\frac{(1/y)\ (dy/dt)}{(1/x)\ (dx/dt)} = b: \text{ growth coefficient}$$

which illustrates mathematically, how the coefficient 'b' represents the ratio of specific growth rates of the two components which are being related by the equation. This ratio must stay constant, if the

use of the equation is to be justified. The assumption of such constancy was first criticized by the Cambridge workers and most recently by McDonald et al. (1977) and Taylor (1978). Taylor pointed out that log-log relationships would nearly always be curved over extended periods of growth, and thus it was essential to specify the time limits, within which the relationship was claimed to hold. Another criticism of his was, that, due to over-emphasis on the early points and compression of late points, the estimates usually emphasised relative growth rates at early stages and could obscure non-linearity at later stages.

These valuable comments, as well as earlier criticisms of the allometric approach were kept in mind during the present analysis. Thus we have compared estimates yielded by the equation with original unadjusted group means and looked at changes in differential growth ratios over the experimental ranges. Genotype or treatment differences were always tested for.

The initial approach to any regression analysis was always to test for improvement of fit by including a quadratic term, thus changing the equation to:

$$\log y = \log a + b_1 \log x + b_2 (\log x)^2$$

When quadratic effects were found to approach significance, their elimination was attempted by subdividing the experimental periods and calculating separate coefficients for smaller time intervals, However, when persistent, the quadratic term was included in the final model. In such cases, changes in the b coefficient could be estimated by differentiation of the quadratic equation, changing the value of x:

$$b = b_1 + 2b_2 x$$

Differences between growth coefficients, from one interval to another, were tested by the student's t-test. When there were common groups to both intervals, i.e. the last group in interval I was the first group in interval II, the coefficient estimates could not be assumed to be independent of each other. In such cases it can be shown that:

$$SE_{(diff.)} \leq SE_{(bI)} + SE_{(bII)}$$

and this standard error was used for the significance test.

All regression analysis requires the choice of an independent variable. In our work several independent variables have been used,

depending on the anatomical classification of the components being investigated and these are specified with the presentation of our results.

Carcass composition, tissue distribution and various linear dimensions have been studied by contrasting estimates derived from log-log regressions or by the direct comparison of means at constant ages.

For convenience, all means derived by log-log regressions have been converted to geometric means. To overcome the asymmetry of transformed logarithmic standard errors, approximate estimates were obtained by the formula:

$$SE = (\text{antilog}(\bar{x} + 2\text{s.e})_{\log} - \text{antilog}(\bar{x} - 2\text{s.e.})_{\log/4}).$$

CHAPTER 3.

LIVE WEIGHT GROWTH

3.1. INTRODUCTION

The growing period of farm animals may be conveniently divided into the two phases of pre-natal and post-natal growth. The subtle change in the lamb's environment at weaning perhaps justifies a further division of the latter into the pre- and post-weaning phases.

The weight of the lamb at birth is important for at least two reasons. 1) Peri- and neo-natal viability of lambs is greatly affected by birth weight (Alexander, 1964; Everitt, 1968; Hight and Jury, 1969), lambs of the average weight for the respective breed having better chances of survival than either of the extremes (Purser and Young, 1959, 1964; Pálsson and Thorsteinsson, 1973). 2) Growth rates and weights at later stages have been shown to be directly related to birth weight (De Baca, Bogart, Calvin and Nelson, 1956; Thomson and McDonald, 1956; Campbell, 1963; Butcher, Dunbar and Welch, 1964; Shelton, 1964; Seebeck, 1965; Chopra and Acharya, 1971). Thus, increases of 2.5 - 7 kg in weaning weights of lambs have been reported for each 1 kg increase in birth weight.

Birth weight is affected by breed and other genetical factors, sex, litter size, length of gestation, nutrition, age and size of the dam. The newborn lamb is a combined product of its own genetical constitution and its maternal environment. The relative importance of these effects, in determining size at birth, is of immediate interest to the farmer in relation to his breeding and management policy.

Hammond (1932), Bonsma (1939), Hunter (1956), Dickinson, Hancock, Hovel, Taylor and Wiener (1962) and Wiener and Hayter (1974) have all shown that the larger ewes tend to give birth to heavier lambs. Hunter (1956) concluded from his work, which involved reciprocal crossing of heavy and light breeds, that maternal environment was the dominating factor in this respect, while Dickinson et al. (1962), adopting a similar approach, but using egg transfer, estimated the genotype and maternal components to account for 70% and 24 - 29% of the variation in birth weight, respectively. Evidence for genetic influence on birth weight has also been gained by comparing different sire breeds, when crossed with a common dambreed (Jamison, Carter, Gaines and Kincaid, 1961; Seebeck, 1965; Kellaway, 1973). However,

the heritability estimates of birth weight are generally low (Blackwell and Henderson, 1955; Bichard and Yalcin, 1964).

Wallace (1948) clearly demonstrated that restricted nutrition of the ewe in late pregnancy can grossly retard foetal growth and result in smaller lambs being born. He also showed this effect to be stronger on twins and triplets than on single lambs. These findings have later been verified by several workers (Guyer and Dyer, 1954; Treacher, 1970). While Wallace (1948) did not find nutrition, during the first three months of pregnancy, to affect foetal growth at that stage, or birth weight, such effects have been reported in Merino sheep by Everitt (1964, 1966).

Young ewes give birth to lighter lambs than mature ones (Pålsson, 1955; Hunter, 1956; Chopra and Acharya, 1971). The reason is most likely a nutritional one, as the immature ewes are still growing and their tissues are thus in competition with the foetus for available nutrients.

It is widely recognised, that singles are born heavier than twins and further reduction in birth weight is associated with increasing litter size (Wallace, 1948; Blackwell and Henderson, 1955; Jamison et al., 1961; Seebeck, 1965; Donald and Russel, 1970; Robinson, McDonald, Fraser and Croft, 1977). Relative weight differences, due to type of birth, appear to vary among breeds, although direct comparisons of the different sources may be misleading. In the Iceland sheep, single males may weigh 30% more than twin males at birth (Pålsson and Thorsteinsson, 1973). There is little doubt that the major factor involved is nutrition.

Sexual differences in birth weight are well known for sheep. Males are generally born heavier than females (Jamison, 1961; Seebeck, 1965) and reach higher ultimate weights.

Postnatal growth. Bonsma (1939) stated that the rate of growth was genetically controlled, while subject to envorinmental modifications. In general, the heaviest breeds of sheep show the highest absolute gains (Widdowson and Kennedy, 1962), resulting in a greater variation in live weights at later stages than at birth (Bowman, 1968). However, the growth rate needs not be directly proportional to adult live weight. Thus, Boyd, Doney, Gunn and Jewell (1964) and Wiener (1967) found several different breeds to reach variable proportions of their mature weights within the first year of life. Such comparisons must,

however, always be valued in light of the environmental conditions, under which the results are obtained, and these were not identical for all the breeds in the case of Boyd et al. (1964).

Breed differences in growth rate need not be indicative of differences in genetic growth capacity, as important breed characteristics, such as milking ability, must not be disregarded. Nevertheless, there is sufficient evidence, from crosses of different sire breeds with a common dam bred, to conclude that breed differences exist in this respect (Bell, Madsen, Bennett, Madsen and Schmutz, 1950; De Baca et al, 1956; Bailey, Chapman and Pope, 1961; Seebeck, 1965; Donald, Read and Russel, 1970). Intra-breed genetic influences have most often been studied in terms of heritability estimates of pre-weaning growth rate or weaning weight. Such estimates are generally low, but depend greatly upon the method of estimation, as well as on the extent of adjustment for important environmental factors (Bowman, 1968). Sire effects have been reported to account for 6% of the variation in growth rate of their progeny (Campbell 1963; Broadbent and Watson, 1967) and a difference of 10% was observed by Broadbent and Bowman (1964) between the progeny of the best and the worst Suffolk ram in a progeny trial.

When ranking different types of animals with respect to their ability to grow, it is necessary that the experimental conditions be specified, as significant genotype - environmental interactions may exist. This is particularly important, when animals of vastly different sizes are being compared. For instance, Guyer and Dyer (1954) found heavy Hampshire rams to give faster growing singles than light rams of the same breed, while there was no significant difference in growth rate of twins, sired by the two types. It would appear, that the less plentiful nutrition of the twin lambs, did not allow the genetic difference in growth potential to be expressed.

The most important single factor, affecting growth of lambs in early life, is the milk supply of the dam. Hunter (1956) showed that a strong relationship existed between milk consumption and the rate of growth, for the first two months of life, but was insignificant thereafter, indicating the increasing ability of the lamb to utilize other food sources. The faster growth of singles than twins, which is well recognized (Hammond, 1932; Hunter, 1956; Campbell, 1963; Donald et al., 1970; Pálsson and Thorsteinsson, 1973), is undoubtedly

the result of better nutrition during the period, in which the lambs are most dependent on their mothers' milk. This is clearly demonstrated by the increased growth rate of twins, when reared as singles (Smith and Lidvall, 1964; Seebeck, 1965; Pálsson and Thorsteinsson, 1973). The fact that such lambs grow slower than singles, can also be explained by a difference in milk consumption, which has been shown to be correlated with birth weight (Guyer and Dyer, 1954). Hammond (1932) found that after two months of age, twins began to grow faster than singles, which coincides with the time, when dependency on milk is rapidly falling.

Several experiments have been conducted to study the effects on live weight growth of restricting the level of nutrition at different stages of the growing period (Pomeroy, 1955; Gunn, 1964; Bradford and Spurlock, 1964; Allden, 1968). In general, such restriction has been found to retard the rate of growth, but when the animals have been changed over to a high plane feeding, they have shown great recuperative capacity and grown faster than unrestricted animals of the same age. The ultimate effect on body weight depends upon the stage at which retardation occurs, as well as on the severity and length of time of the retarding treatment.

Sex plays an important part in the pattern of growth, through inherent genetic differences and the effects of sex hormones. In sheep, males grow faster than castrates (Hammond, 1932; Bradford and Spurlock, 1964) which grow faster than females (Pálsson and Vergés, 1952; Ray and Kromann, 1971). Pálsson and Vergés (1952) found the difference in growth rate, between sexes, only to be apparent when the nutritional plane allowed 'normal' growth. In accord with this is the finding of Large and Taylor (1954), that sex differences were much smaller for twins than singles.

In conclusion, it may be stated that genetic or sexual influences on growth rate are subject to environmental control, which may not affect the different genotypes or sexes in the same manner. The dominating factor is nutrition and, for the lamb, this will be controlled by maternal ability, competition from littermates and naturally or artificially imposed feeding levels. Current findings should be considered accordingly.

3.2. RESULTS

Live weight growth and feed consumption data have been compared by regression analysis, as well as by direct comparisons of means. The main emphasis in the Edinburgh trial was on post-weaning growth of the three cannon bone lines, as affected by different levels of nutrition, while the Icelandic trial was primarily concerned with growth before and immediately after weaning.

a) Birth weight and pre-weaning growth.

Only male lambs (castrated at 8 weeks) were used for growth analysis in the Edinburgh trial. Birth weights, weaning weights and pre-weaning growth rates are shown in table 3.2.1. Since most of the lambs were born and reared as singles, the type of birth had no significant effects on performance. Similarly, age at weaning had little effect. Consequently, the data has not been adjusted to account for either of these factors.

Table 3.2.1. Effect of cannon line on birth weight, weaning weight and pre-weaning growth rate. (Edinburgh).

LINE	LONG		CONTROL		SHORT	
PARAMETER	Mean	SE+	Mean	SE	Mean	SE
No. of lambs	44		45		33	
Birth weight (kg)	3.40	0.116	3.17	0.112	3.20	0.134
Weaning weight (kg)	21.2[a]	0.628	20.66[a]	0.606	18.33[b]	0.722
Daily gain (g/d)	131[a]	4.5	131[a]	4.3	112[b]	5.2
Age at weaning (days)	136	2.1	133	2.0	135	2.4

+) In this and subsequent tables, means with different superscripts differ significantly ($P < 0.05$).

While L-lambs were born on average 200 g heavier than either the C- or S-lambs, this difference was non-significant. However, the 19 g/d superior growth rate of the L- and C-lambs resulted in 2.9 and 2.6 kg heavier weaning weights of these lambs, compared with the S-lambs, a finding that is consistent with previous experience with these lines (Purser, 1980).

In Iceland, the outstanding difference between the two conformation types was that in birth weight. There were no sex x type interactions in birth weight or in any subsequent live weights. The means for types and sexes are presented in tables 3.2.2. and 3.2.4., respectively. The growth curves for each type are further illustrated in figure 3.2.1. L-lambs were born significantly heavier ($p < 0.001$) than the S-lambs, the difference being 0.5 kg (17%) for twins and 0.8 kg (20%) for singles. In order to seek an explanation for this effect, reciprocal crosses were made between the two types in 1980 and the birth weights of those lambs are shown in table 3.2.3. These were similar to the means of the previous two years and would suggest that maternal environment was the causative factor for type differences, as SL-lambs born to L-ewes were similar in weight as LL-lambs and vice versa.

Despite this large difference in birth weight, pre-weaning growth rates were similar for lambs of both types and differences in weaning weight were non-significant for both singles and twins (tables 3.2.2. and 3.2.5.) However, the L-lambs grew slightly (though non-significantly) faster for the eight weeks period after weaning, resulting in a difference of 2.2 kg ($p < 0.05$) for twins and 4.6 kg ($p < 0.05$) for singles at 24 weeks of age. This might indicate that a greater growth potential of the L-lambs had been suppressed by inadequate nutrition at the earlier stage.

Males were born heavier than females and grew faster, resulting in differences of 1.6 kg ($p < 0.05$) and 2.2 kg ($p < 0.05$) in weaning weight and 3.2 kg ($p < 0.01$) and 3.1 kg ($p < 0.05$) at 24 weeks, for twins and singles, respectively. There was no evidence for a greater sex difference among singles than twins.

Table 3.2.5. shows the regressions of pre-weaning weights on age, separately for each year, type, sex and type of birth. These estimates are similar to, but not identical with, average daily gains as calculated by the difference of weaning weight and birth weight. It will be seen

Table 3.2.2. Effect of conformation type on live weight growth from birth to 24 weeks[+] (Iceland).

PARAMETER	CONF. TYPE	TWINS No.	TWINS Mean	TWINS SE		SINGLES No.	SINGLES Mean	SINGLES SE	
Birth wt. (kg)	L	51	3.43	0.067	***	12	4.76	0.143	**
	S	49	2.94	0.068		8	3.93	0.173	
Weaning wt. 16 wks. (kg)	L	51	28.68	0.445	N.S.	12	35.33	0.948	N.S.
	S	49	27.53	0.453		8	34.92	1.147	
24 wks. wt. (kg)	L	28	39.98	0.698	*	7	46.94	1.498	N.S.
	S	25	37.80	0.737		4	42.36	1.904	
Daily gain (g) Birth - 16 wks.	L	51	233	3.9	N.S.	12	281	8.3	N.S.
	S	49	227	4.0		8	289	10.1	
Daily gain (g) 16 - 24 wks.	L	28	177	8.4	N.S.	7	177	18.1	N.S.
	S	25	165	8.9		4	124	23.0	

*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

+ Means adjusted for year and sex effects

Table 3.2.3. Birth weights of twin lambs (adjusted for sex) from reciprocal crosses between L- and S-conformation types, born in 1980 (Iceland).

		SIRE TYPE: LONG Mean (kg)	LONG SE	SHORT Mean (kg)	SHORT SE
DAM TYPE	L	3.44^{a}	0.099	3.45^{a}	0.086
	S	3.02^{b}	0.084	3.09^{b}	0.084

Table 3.2.4. Effect of sex on live weight growth from birth to 24 weeks (Iceland).

	Sex	TWINS No.	Mean	SE		SINGLES No.	Mean	SE	
Birth wt. (kg)	M	47	3.31	0.071	*	8	4.18	0.259	N.S.
	F	53	3.08	0.065		12	4.17	0.221	
Weaning wt. 16 wks. (kg)	M	47	28.88	0.479	*	8	34.77	1.747	N.S.
	F	53	27.29	0.443		12	32.53	1.491	
24 wk.wt. (kg)	M	25	40.41	0.753	**	4	45.84	2.020	N.S.
	F	28	37.36	0.729		7	42.77	1.732	
Daily gain (g) Birth - 16 wks.	M	47	236	4.2	*	8	288	15.3	N.S.
	F	53	224	3.9		12	267	13.0	
Daily gain (g) 16 - 24 wks.	M	25	181	9.2	N.S.	4	152	24.8	N.S.
	F	28	161	8.9		7	147	21.2	

+ Means adjusted for effects, year and conformation type

Table 3.2.5. Linear regressions of live weight on age, from birth to weaning, for year, conformation type, sex and type of birth(Iceland).

Effect		Growth rate(g/d)	SE	
Year	1978	280	3.3	***
	1979	261	4.3	
Conf. type	Long	271	3.3	N.S.
	Short	270	3.5	
Sex	Male	278	3.5	**
	Female	264	3.3	
Birth type	Single	301	5.7	***
	Twin	241	2.4	

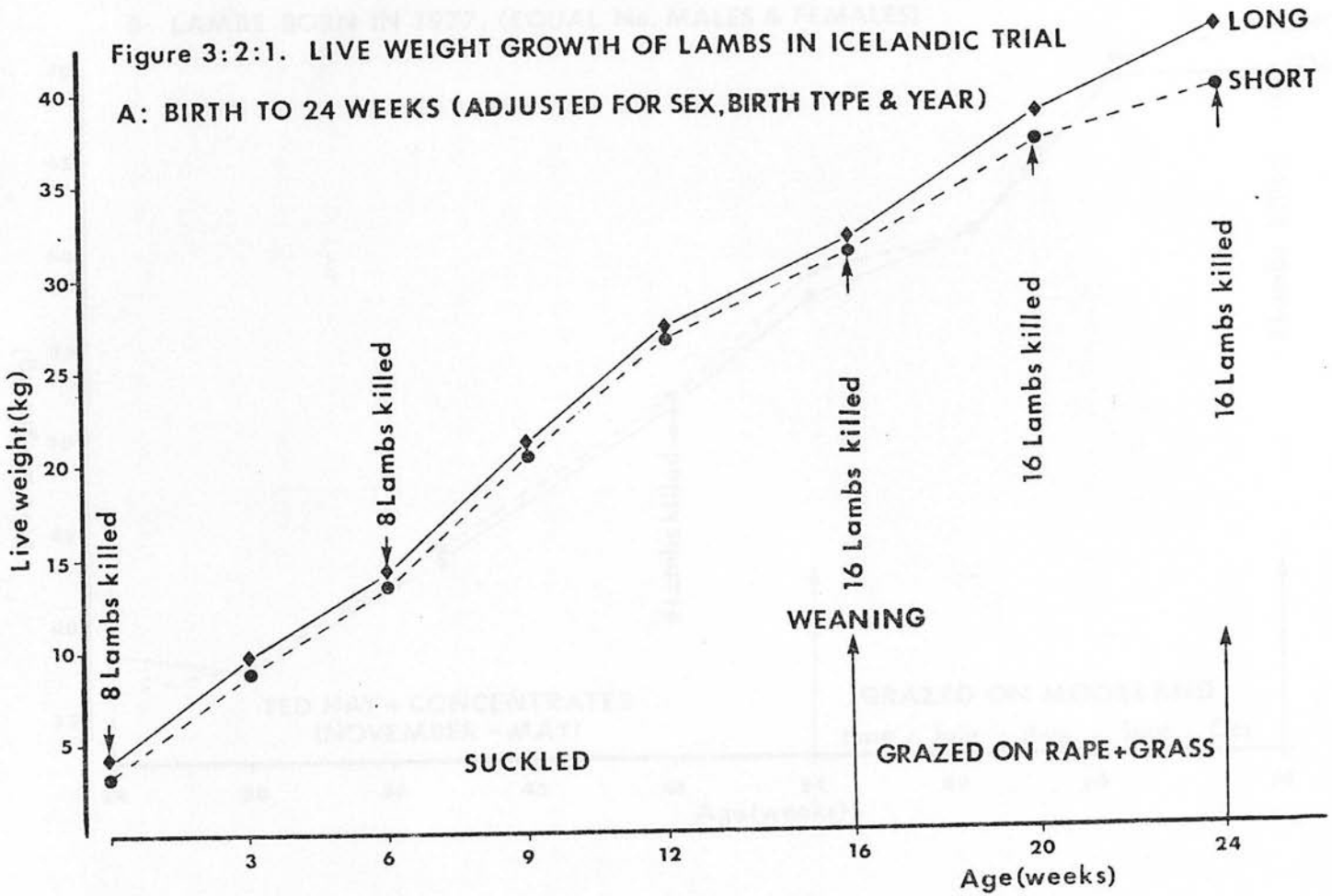


Figure 3:2:1. LIVE WEIGHT GROWTH OF LAMBS IN ICELANDIC TRIAL
A: BIRTH TO 24 WEEKS (ADJUSTED FOR SEX, BIRTH TYPE & YEAR)
LONG
SHORT
Live weight (kg)
40
35
30
25
20
15
10
5
8 Lambs killed
8 Lambs killed
16 Lambs killed
16 Lambs killed
16 Lambs killed
WEANING
SUCKLED
GRAZED ON RAPE+GRASS
3
6
9
12
16
20
24
Age (weeks)

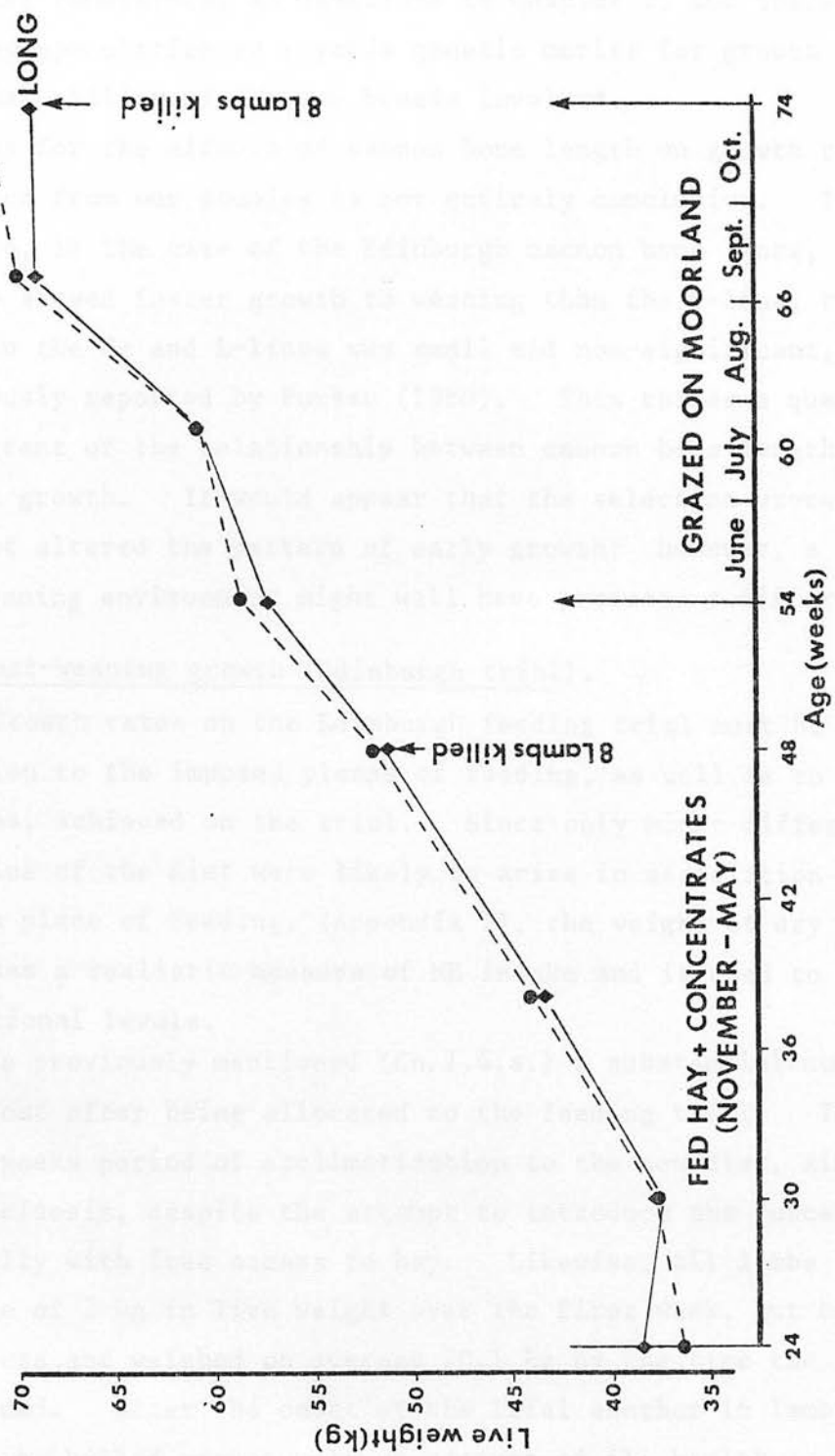


Figure 3:2:1. (Continued)

B: LAMBS BORN IN 1977. (EQUAL No. MALES & FEMALES)

that relative differences between types and sexes are similar, which ever method is applied. The lower growth rates in 1979 simply reflect a colder summer with poorer pasture growth.

In comparing the results from the two trials, it is evident that the Icelandic lambs were born heavier and grew faster than the Edinburgh lambs. The most obvious reason lies in the entirely different environmental conditions, as described in Chapter 2, and there is no scope for any speculation as regards genetic merits for growth capacity or maternal ability of the two breeds involved.

As for the effects of cannon bone length on growth rate, the evidence from our studies is not entirely conclusive. It is interesting to note, in the case of the Edinburgh cannon bone lines, that while the C-line showed faster growth to weaning than the S-line, the difference between the C- and L-lines was small and non-significant, as was previously reported by Purser (1980). This raises a question regarding the extent of the relationship between cannon bone length and live weight growth. It would appear that the selection procedure in Iceland had not altered the pattern of early growth; however, a more favourable pre-weaning environment might well have produced a different result.

b) Post-weaning growth (Edinburgh trial).

Growth rates on the Edinburgh feeding trial must be considered in relation to the imposed planes of feeding, as well as to the actual feed intakes, achieved on the trial. Since only minor differences in the ME-value of the diet were likely to arise in association with differences in the plane of feeding, (Appendix 1), the weight of dry matter consumed provides a realistic measure of ME intake and is used to indicate nutritional levels.

As previously mentioned (Ch.2.4.a.) a substantial number of lambs were lost after being allocated to the feeding trial. Thus, over the three weeks period of acclimatization to the new diet, six lambs died from acidosis, despite the attempt to introduce the concentrate diet gradually with free access to hay. Likewise, all lambs lost an average of 2 kg in live weight over the first week, but had regained that loss and weighed on average 20.1 kg by the time the feeding trial commenced. After the onset of the trial another 16 lambs were lost or had to be killed prematurely on account of ill health. The most significant factor contributing to these losses was the incidence of

urinary calculi, which was first identified in the flock two months after the trial commenced. The apparent cause was a mineral imbalance of the diet, as increasing the level of NaCl and Ca, while reducing that of Mg, immediately cured the problem. Nevertheless, 12 lambs died or were killed as a result of this problem, and four lambs died of other causes, bringing the total to 16. Six of those were killed at an early stage of disease, before intake had fallen markedly or weight had been lost, and are included in subsequent analyses. These unfortunate losses, however, upset the balance of the initial design and left several cells represented by only one lamb (see table 2.4.1.)

An other major complicating factor in the analysis of the present data was the great variation in individual intakes which were achieved throughout the trial. This resulted in considerable overlap between all three feeding planes and differences between cannon lines. A partial explanation lies in the initial variation that existed in live weight. Under the circumstances, a weight-based feeding regime, taking account of individual variation, would probably have been more appropriate. The effects of vastly different intakes and growth rates, within planes, were precipitated by pre-allocating the lambs to slaughter groups, which often meant that the lambs killed at a particular stage were not representative, in weight, of the corresponding line x plane population, thus causing irregularity of intra-plane growth curves. Another effect of the pre-allocation was, in some instances, to cause irregular time intervals between slaughter points (table 3.2.6.), as a result of different mean growth rates being achieved by the different slaughter groups within the same plane of feeding.

Table 3.2.6. Time on trial, from onset to slaughter, and the mean slaughter weight of each group.

Group	High plane		Med.plane		Low plane	
	Time (wks.)	Wt. (kg)	Time (wks.)	Wt. (kg)	Time (wks.)	Wt. (kg)
30 kg	8	30.2	10	29.8	13	30.0
35 kg	12	36.2	15	35.0	16	34.8
41 kg	18	40.8	20	40.9	21	40.1
46 kg	20	46.3	26	46.0	29	46.3
Mat.	74	82.7				

The growth data have been analysed in two ways. Firstly, by the regression of live weight on time, or cumulated feed intake and, secondly, by comparisons of average daily gains, or ratios of gains to intakes, from onset of trial to slaughter. The unadjusted feed intake and live weight data have been plotted in figures 3.2.2. and 3.2.3., respectively.

Table 3.2.7. shows the mean daily D.M. intakes, for each line and plane, over two 100 day intervals with cumulated 200 day D.M. intakes, as estimated by regression equations. The 200 day period was chosen as a convenient compromise between the final dates of M- and L-plane lambs, only the H-maturity group staying on trial beyond this time. From table 3.2.7. the changes in intake with time are clearly apparent. It is also evident that there were considerable line differences in D.M. consumption throughout the trial and that the patterns of increase were somewhat variable. The overall effect was such that after 100 days the L-lambs had consumed on average 7% and 12% more than C- or S-lambs ($p < 0.05$), respectively while the 200 day consumption was approximately 10% higher for L- and C-lambs than for the S-lambs ($p < 0.01$), there being little difference between the former.

The daily live weight gains are presented in table 3.2.8. The two methods of estimation yielded comparable results as regards the overall rate of growth. However, while non-significant, the two sets of unadjusted results showed different orders of merit, which could be due to a bias caused by the uneven distribution of lambs between slaughter points. Such a bias is likely to be of a greater significance in the directly calculated daily gains, than in the regressional analysis; however, it should be accounted for in the adjusted results.

In line with the greater intakes, there was clearly a tendency for L-lambs to grow faster than S-lambs, especially on the high plane, but the differences were non-significant. However, when growth rates were adjusted to a constant level of daily D.M. intake and to equal time on trial, S-lambs showed the highest rates of gain, although only significantly so in comparison to C-lambs. This trend is repeated (table 3.2.9.) when the efficiency of feed conversion into live weight gain is compared. The apparent advantage of the S-lambs is most likely the result of these lambs having been lighter in weight, thus requiring less for maintenance and having more energy available for growth. Table 3.2.9a. shows clearly how the ratio of live weight gain to D.M. consumption declined

Figure 3:2:2. CUMULATED FEED (DM) CONSUMPTION ON THE EDINBURGH FEEDING TRIAL. (UNWEIGHTED MEANS OF 3 FEEDING PLANES)

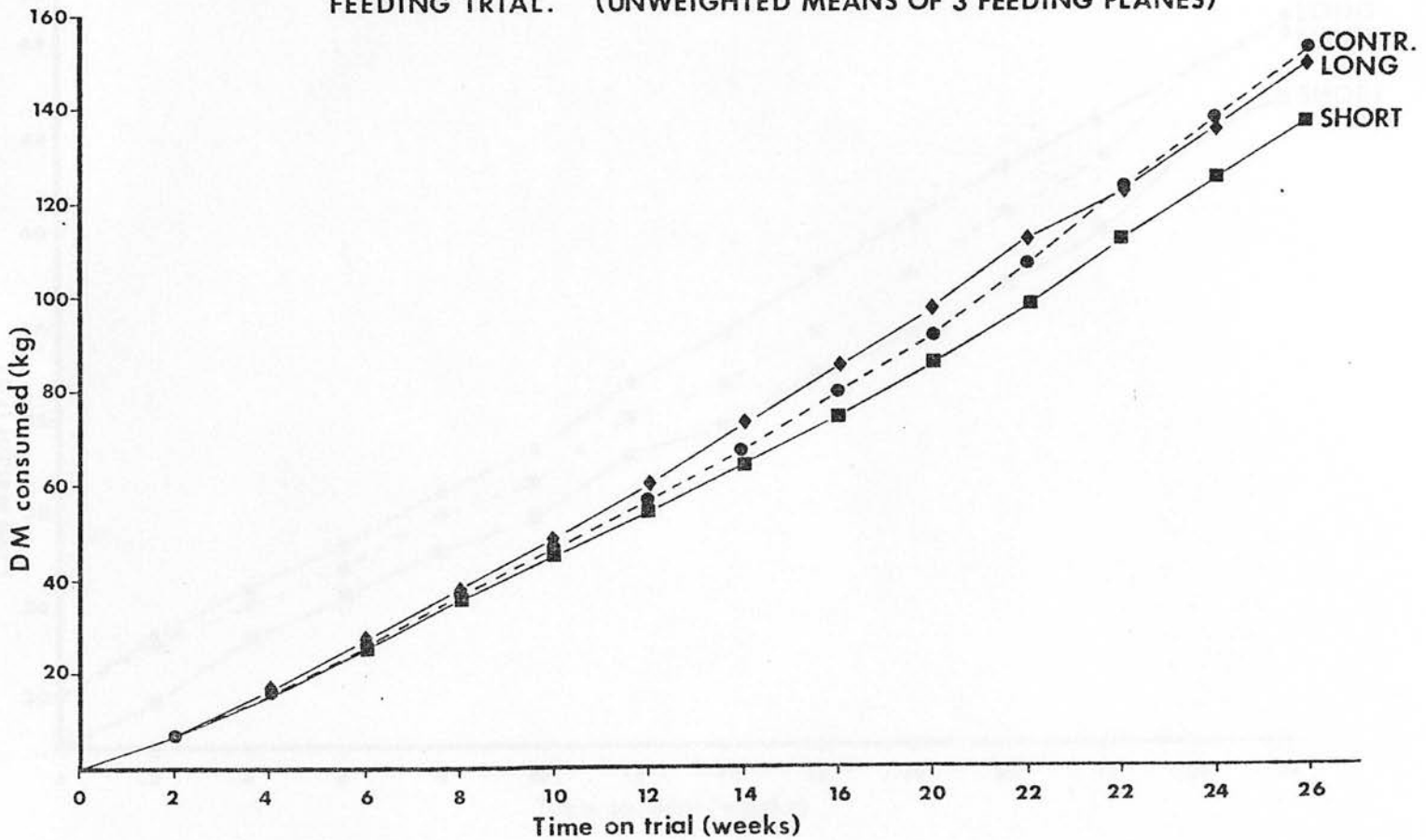


Figure 3:2:3. LIVE WEIGHT GROWTH OF LAMBS ON THE EDINBURGH FEEDING TRIAL.
(UNWEIGHTED MEANS FOR 3 FEEDING PLANES)

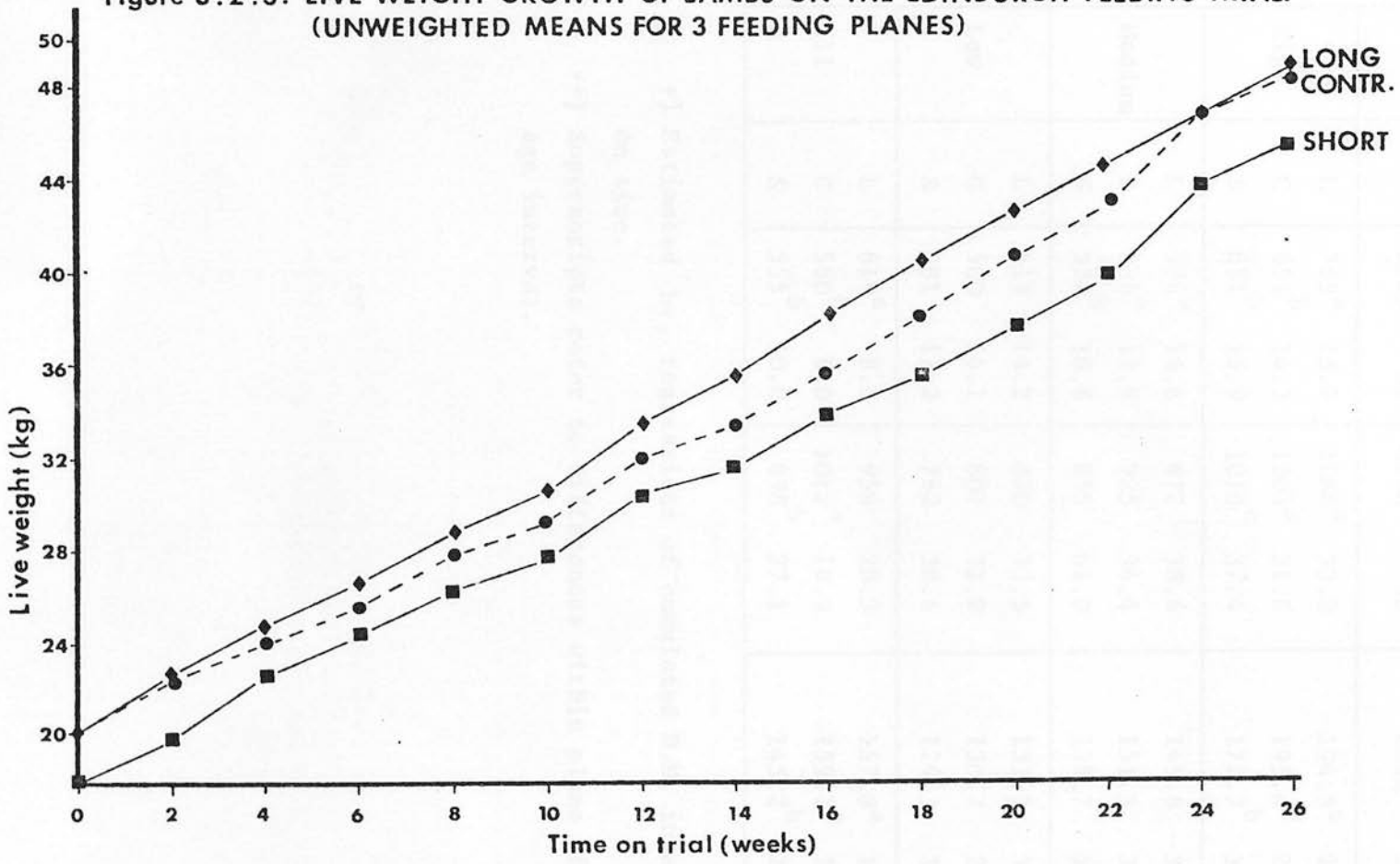


Table 3.2.7. Effect of cannon line on dry matter consumption[+] (g/day) (Edinburgh).

Plane	Line	Mean daily intake for: Days 1-100 Mean[++]	SE	Days 101-200 Mean	SE	Total D.M. consumption 200 days (kg) Mean	SE
High	L	759[a]	15.7	1186[a]	33.2	194.5[a]	2.93
	C	651[b]	14.3	1303[b]	31.8	195.4[a]	2.84
	S	651[b]	15.9	1076[c]	37.4	172.7[b]	3.39
Medium	L	584[a]	14.6	872	38.6	145.6	3.57
	C	588[a]	12.9	925	34.4	151.3	3.19
	S	532[b]	18.8	855	61.0	138.7	5.80
Low	L	513	14.2	820	33.5	133.3	3.03
	C	500	14.1	807	31.8	130.7	2.85
	S	481	17.2	762	38.6	124.3	3.46
All	L	619[a]	8.6	959	20.3	157.8[a]	1.84
	C	580[b]	8.0	1012[a]	18.9	159.1[a]	1.71
	S	555[b]	10.0	898[b]	27.1	145.2[b]	2.52

+) Estimated by, regressions of cumulated D.M. intake on time.

++) Superscripts refer to differences within plane of feeding x age interval.

Table 3.2.8. Effect of cannon line on post-weaning growth rates (g/day) (Edinburgh).

Plane	Line	Mean+	SE
High	L	177	7.4
	C	174	6.6
	S	165	8.0
Medium	L	134	7.6
	C	136	7.0
	S	127	11.5
Low	L	131	7.8
	C	124	6.9
	S	130	8.8
All	L	147 (158)	5.0 (4.3)
	C	145 (147[a])	3.9 (4.1)
	S	141 (165[b])	5.5 (5.8)

+) Regression coefficients of live weight on time.

Values in parantheses derived from slaughter wt.- initial wt/time and adjusted for daily intake and time on trial.

Table 3.2.9. Effect of cannon line on post-weaning feed conversion efficiency (Gain (g)/D.M. consumed (kg)). (Edinburgh).

A: Estimated by regressions+.

Line	On day 1	SE	On day 100	SE
Long	212	13.1	183	8.2
Control	216[a]	12.1	174[b]	8.0
Short	226	17.7	184	14.2
All	218[a]	8.4	180[b]	6.1

+) Live wt. regressed on cumulated D.M. intake and adjusted for plane of feeding.

B: Means of individual feed conversion from onset of trial to slaughter+.

Line	Mean	SE
Long	201	5.4
Control	194	5.0
Short	206	6.2

+) Adjusted for time on trial, after which daily D.M. intake had no effect.

with time, from 218 g/kg on day 1 to 180 g/kg on day 100 ($p < 0.01$). This is probably the result of increasing deposition of fat in the gain, as the animals grew heavier, since fat growth is more energy demanding than lean growth (Webster, 1976; Béranger, 1978).

It is not possible to draw any firm conclusions from the results as regards the inherent growth capacity of the three genetic lines under study. Line differences in appetite can, at least partly, be explained by differences in initial live weight. Once these have been removed, there is no consistent evidence for a relationship between cannon bone length and rate of growth or the gross efficiency of converting feed into live weight.

CHAPTER 4.

GROWTH AND DEVELOPMENT OF THE 'EMPTY' BODY

4.1. INTRODUCTION

The relative growth of the carcass, various body parts and organs of sheep, has been studied in detail by Hammond (1932), Wallace (1948), Pálsson and Verges (1952), Wardrop (1960), Wardrop and Coombe (1960), Fourie (1965), Everitt and Jury (1966a) and Kirton, Fourie and Jury (1972). From these studies the following pattern of development has been established: 1) The carcass grows at a slightly higher rate than the empty body, resulting in the increase of dressing percentage with age. At the same time the head, pelt and feet decline as proportions of body weight, the feet showing the least weight increase after birth. The relationship of the empty body, or the carcass, with live weight is, however, subject to variation in alimentary tract contents. Thus there is a gradual decline in dressing percentage over the phase of rapid development of ruminant function, associated with the change in dietary composition, which results in an increased proportion of gut fill in the live weight. 2) The various body organs exhibit marked differential growth rates in post-natal life. The brain has the slowest relative growth, followed closely by the eyeballs. Most internal organs grow at a lower rate than the whole body, including the thoracic organs and liver. Wallace (1948) found these organs to have their periods of highest growth intensity in pre-natal life or immediately after birth. This is not so, however, for the alimentary tract, sex organs and internal fat depots all of which grow relatively faster than the body post partum. 3) Differential patterns are observed within the alimentary tract, the rumen showing the highest and the abomasum the lowest relative growth rates. Wardrop and Coombe (1960) found the rumen in the grazing lamb to grow at its highest rate from birth to nine weeks of age, while the four stomachs had almost reached their adult relative proportions at eight weeks. Stomach development is, however, greatly affected by the nature of the early diet (Wardrop, 1960). The different abdominal fat depots also show differential growth patterns after birth. Thus caul fat increases proportionately most, followed by mesenteric fat and kidney fat in respective order.

Pálsson (1955) pointed out that, in general, the order of development of the various body organs could be described in terms of

changes in functional demands as the animal grows. Thus there is clearly a need for well developed brain, eyes, lungs, kidneys, oesophagus, abomasum and small intestine to perform vital functions immediately after birth, while organs like the rumen, reticulum and sex organs have unimportant functions until some time after birth. This concept of functional demand has been widely used in explaining growth phenomena (Fowler, 1968; Berg and Butterfield, 1976).

Breed effects on relative growth rates of body components were demonstrated by Kirton et al. (1972), reanalysing the data of Fourie (1965). The comprehensive study by Fourie is of particular interest to the present work, as the breeds involved, namely the Southdown, New Zealand Romney and their cross, represent vastly different types of conformation and thus provide a useful basis for comparison with the present results. The carcass, head, heart, lungs, penis, omental fat, oesophagus and reticulum were among the components exhibiting breed differences in relative growth coefficients in Fourie's work. The carcass grew relatively faster in the Southdown than in the Romney, and thus the difference in carcass weight increased from 4% to 11%, as starved body weight increased from 5 kg to 55 kg. The Southdown also deposited more internal fat, while the Romney had a heavier head, heart and lungs, among other differences.

Sex has been found to influence body development in terms of relative growth rates and proportions of the carcass and non-carcass components. The carcass normally comprises a higher proportion in females than in wethers (Pálsson and Vergés, 1952) or in males (Fourie, 1965; Kirton et al., 1972). However, Pálsson and Vergés (1952) found this situation to be reversed as the animal approaches mature weight. Everitt and Jury (1966a) castrated male and female lambs and found this to reduce the proportion of the carcass in the empty body, the reduction being relatively greater for females than for males. Other differences, demonstrated by their work, included higher specific growth rates of the head for males, than for females, and for entire versus gonadectomized animals. The kidneys grew relatively fastest in males and slowest in wethers. Sex differences in the analysis of Kirton et al. (1972) were largely confined to fat depots and some endocrine glands. Kidney fat, omental fat and mesenteric fat grew relatively faster in the females, as did the adrenals, while the pituitary gland, lungs and head showed higher

relative growth rates in males.

Nutritional effects on the development of the empty body in sheep have been reported by Wallace (1948), Pálsson and Verges (1952), Wardrop (1960) and Morgan and Owen (1972), and in cattle by Seebeck (1967 and 1973a). All these workers found the plane of nutrition, or the nature of the diet, to have differential effects on the various body parts or organs, the nature and extent of which, were often dependent on the stage of growth.

4.2 RESULTS

a) Common developmental patterns.

The empty body can most coarsely be divided into two, i.e. the carcass and non-carcass components, or offal parts. While the current study is primarily concerned with the growth and development of the carcass and its tissues, the offals have been studied in considerable detail too, in order to build up a more complete picture of the development of the body as a whole.

The patterns of relative growth were examined in terms of relative growth coefficients over defined age intervals, which were chosen as to render most quadratic trends statistically non-significant. Thus, the Edinburgh data was analysed in two phases (table 4.2.1.), pre-weaning and post-weaning (on feeding trial), whereas in Iceland, growth coefficients were determined for four age intervals, i.e. birth-6 weeks, 6-16 weeks, 16-24 weeks and 48-74 weeks. These are presented in full in Appendix 7, only a few selected ones being shown with the schematic presentation in figures 4.2.1. and 4.2.3. a-f.

Bearing in mind that the pre-trial coefficients in table 4.2.1. cover the first 19 weeks of life, there is a general and good agreement between the two trials, as far as the anatomical separation of organs was comparable. Thus, the pre-trial coefficients in the Edinburgh experiment almost invariably fall in between those for age intervals 0-6 and 6-16 weeks in the Icelandic trial. There are certain differences apparent in the later phases, some of which can readily be explained by different treatments.

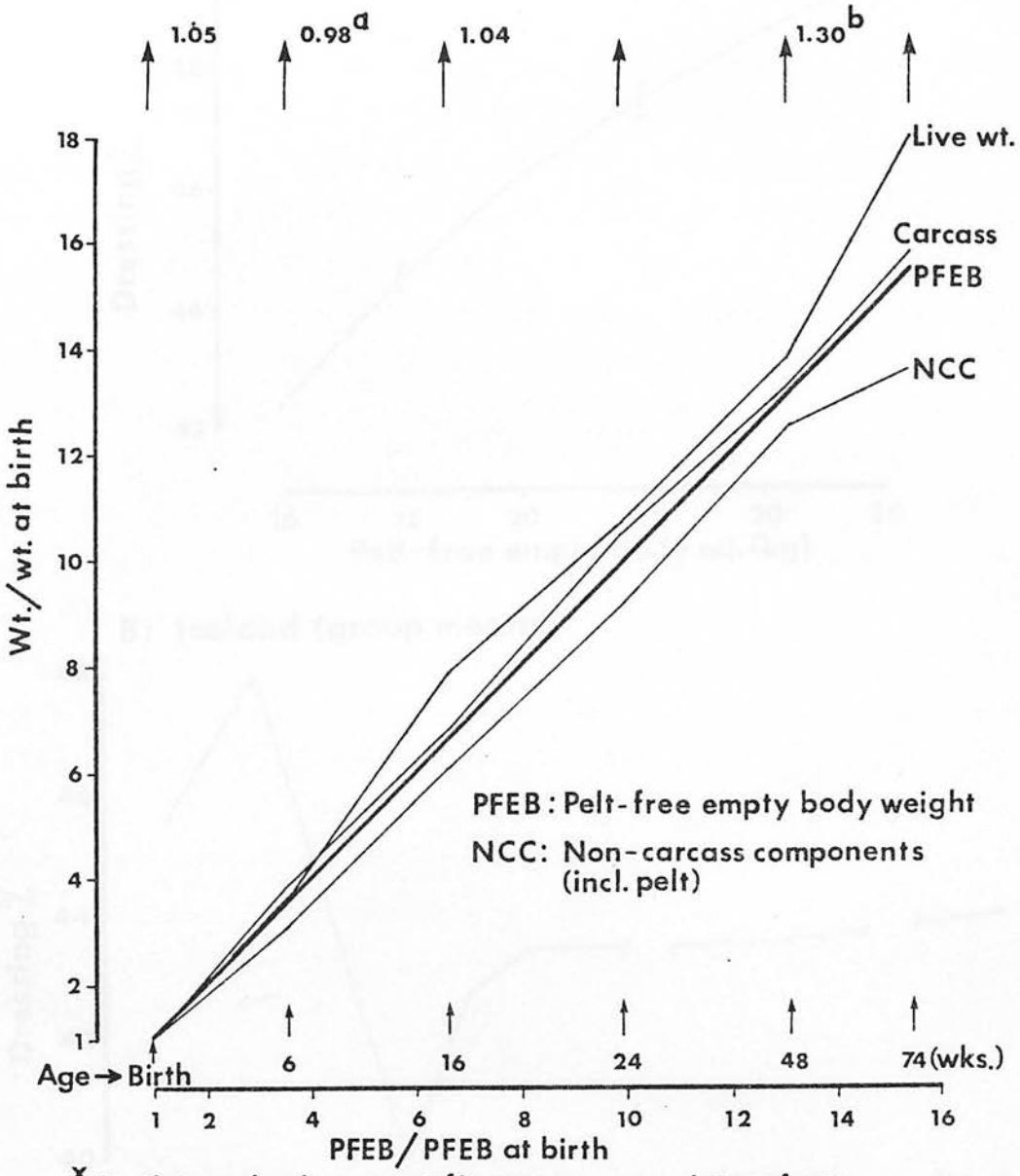
i) The carcass (figure 4.2.1.) grew slightly faster than the pelt-free empty body (PFEB) and increasingly so with age, which is in keeping with previous works. Its relationship with live weight was,

Table 4.2.1. Relative growth coefficients (b) relating weights of body components to pelt-free empty body weight (PFEB). (Edinburgh).

Component	Pre-trial	SE	On trial+	SE	Signif. of diff.
Carcass	1.02	0.011	1.14	0.024	**
Head	0.75	0.012	0.73	0.062	N.S.
Feet	0.58	0.019	0.75	0.042	*
Pelt	0.86	0.033	1.20	0.082	**
Heart	0.50	0.054	0.52	0.065	N.S.
Tot. Thoracic organs	0.71	0.030	0.59	0.078	N.S.
Liver	0.89	0.037	0.44	0.071	***
Kidneys	0.85	0.045	0.36	0.076	***
Alimentary tract	1.28	0.050	(0.05)	0.088	***
Intestinal fat	-	-	3.29	0.206	-
Kidney fat	0.75	0.011	1.55	0.179	***

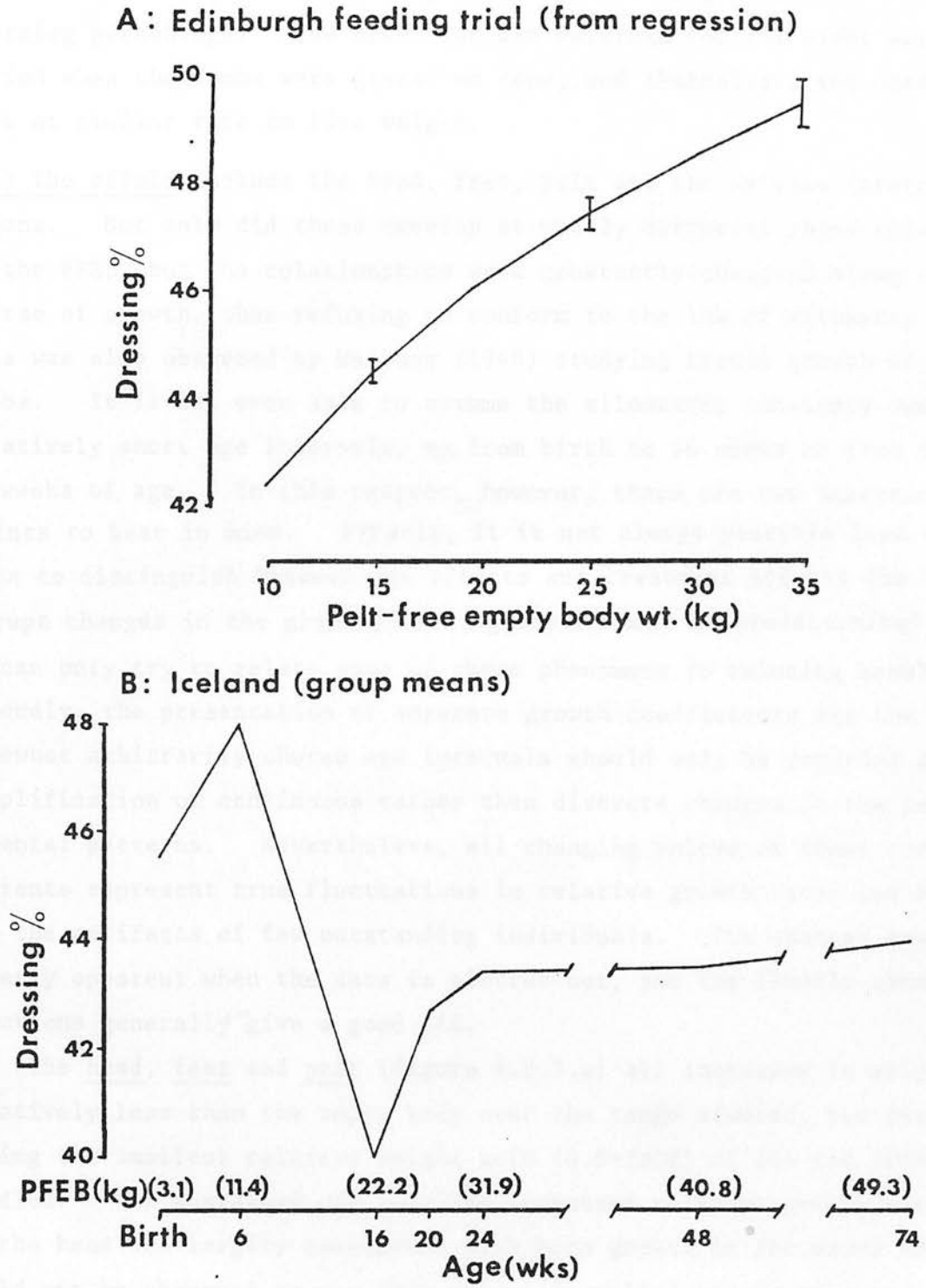
+) Values adjusted to constant daily D.M. intake.

Figure 4:2:1. RELATIVE GROWTH OF LIVE WEIGHT, THE CARCASS AND NON-CARCASS COMPONENTS (ICELAND)



x In this and subsequent figures, superscripts refer to differences between age intervals

Figure 4:2:2. CHANGES IN DRESSING PERCENTAGE WITH AGE/WEIGHT



however, confused by varying amounts of gut fill, as is clearly illustrated in figure 4.2.2. For the first six weeks, before advanced development of ruminant function, dressing percentage was increased by 2.5 units ($p < 0.05$). The subsequent ten weeks coincide with increasing independence of the lambs and falling pasture quality towards the end of the period, resulting in greater amounts of gut fill and reduced dressing percentage. The situation was reversed for the eight weeks period when the lambs were grazed on rape, and thereafter, the carcass grew at similar rate to live weight.

(ii) The offals include the head, feet, pelt and the various internal organs. Not only did these develop at vastly different rates relative to the PFEB, but the relationships were constantly changing along the course of growth, thus refusing to conform to the law of allometry. This was also observed by Wallace (1948) studying foetal growth of lambs. It is not even safe to assume the allometric constancy over relatively short age intervals, eg. from birth to 16 weeks or from 6 to 24 weeks of age. In this respect, however, there are two important points to bear in mind. Firstly, it is not always possible from our data to distinguish between age effects and treatment effects due to the abrupt changes in the grazing/feeding environment at predetermined ages. We can only try to relate some of these phenomena to existing knowledge. Secondly, the presentation of separate growth coefficients for the somewhat arbitrarily chosen age intervals should only be regarded as a simplification of continuous rather than discrete changes in the developmental patterns. Nevertheless, all changing values of these coefficients represent true fluctuations in relative growth rates and are not the artifacts of few outstanding individuals. The changes are clearly apparent when the data is plotted out, and the finally chosen equations generally give a good fit.

The head, feet and pelt (figure 4.2.3.a) all increased in weight relatively less than the empty body over the range studied, the feet making the smallest relative weight gain (4.5-fold) of all the offals studied. The sustained and somewhat increased relative growth rate of the head was largely associated with horn growth in the males and would not be observed to the same extent in polled breeds of sheep.

The thoracic organs (figure 4.2.3.b), on the whole, grew relatively slower than the empty body, the growth coefficient being 0.83 initially and 0.64 in the final period. The thyroids exhibited the most

Figure 4:2:3. RELATIVE GROWTH OF BODY COMPONENTS. (With selected growth coefficients relating to PFEB)

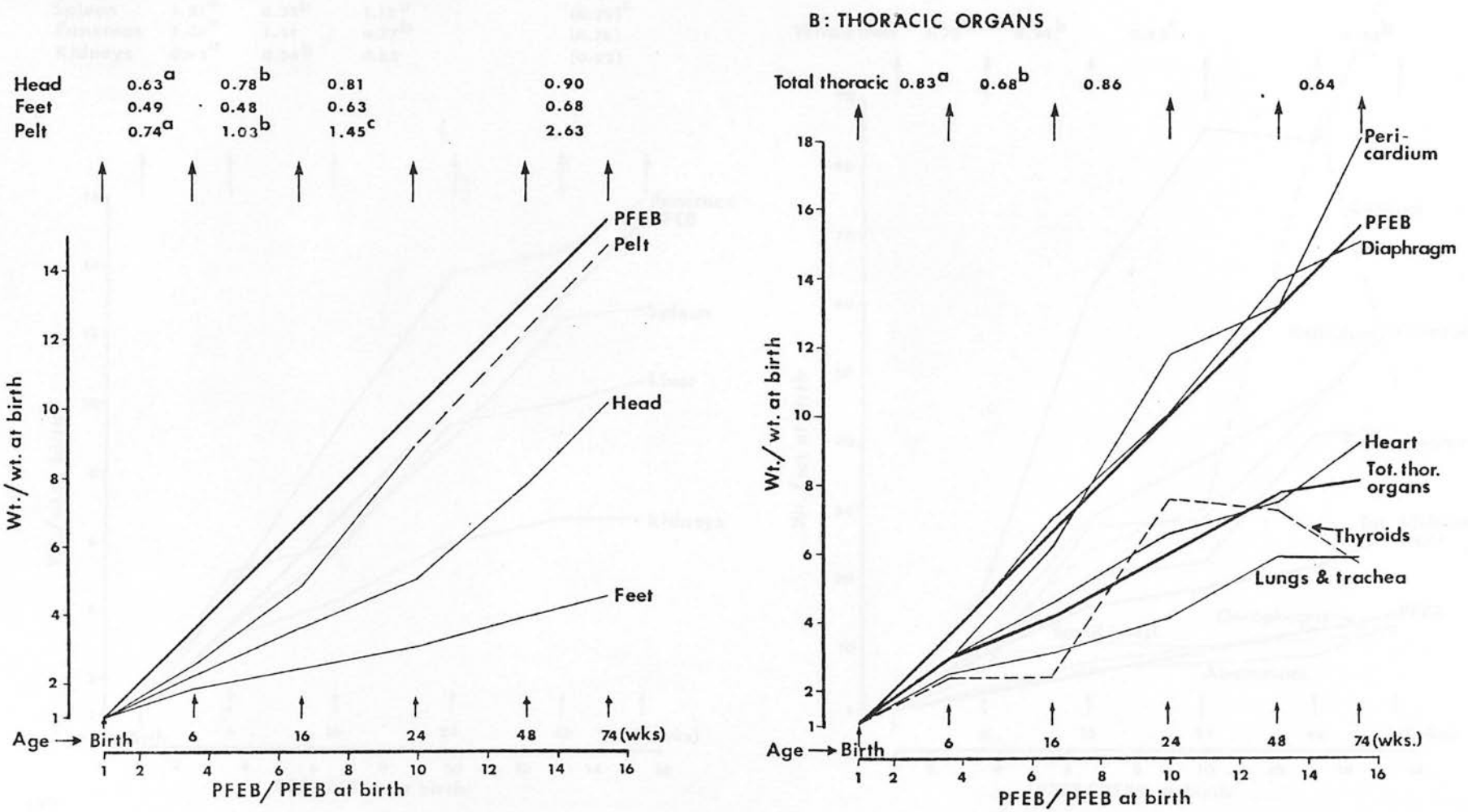
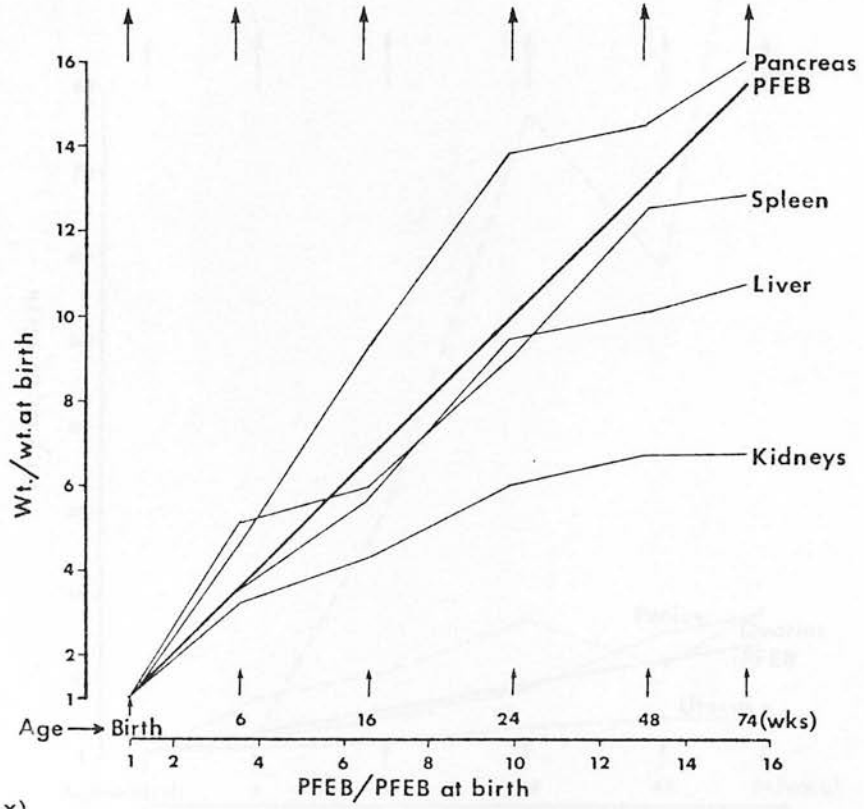


Fig. 4:2:3. Contd.

C: SELECTED ABDOMINAL ORGANS

Liver	1.06^{a}	0.76^{b}	1.31^{a}	0.57^{b}
Spleen	1.31^{a}	0.35^{b}	1.12^{a}	$(0.75)^{x}$
Pancreas	1.30^{a}	1.11	0.77^{b}	(0.78)
Kidneys	0.93^{a}	0.54^{b}	0.83	(0.22)



(x) Values in parenthesis non-significant from 0

D: THE ALIMENTARY TRACT

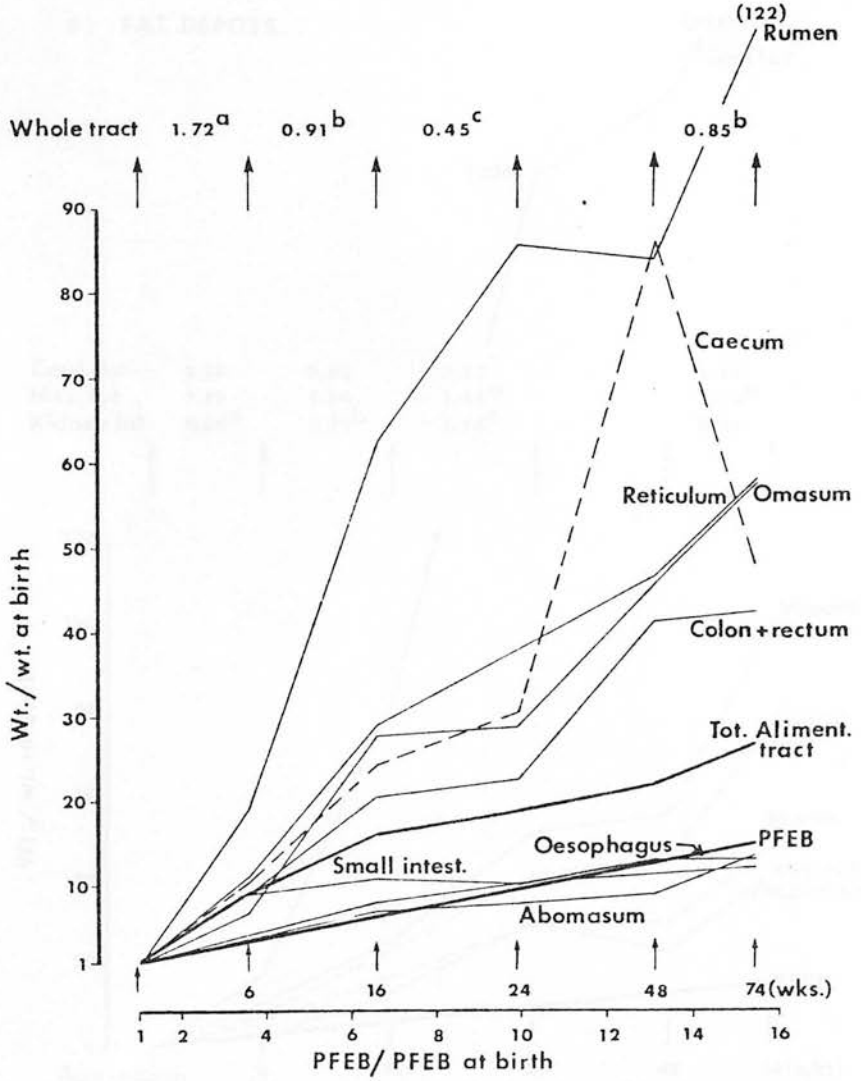
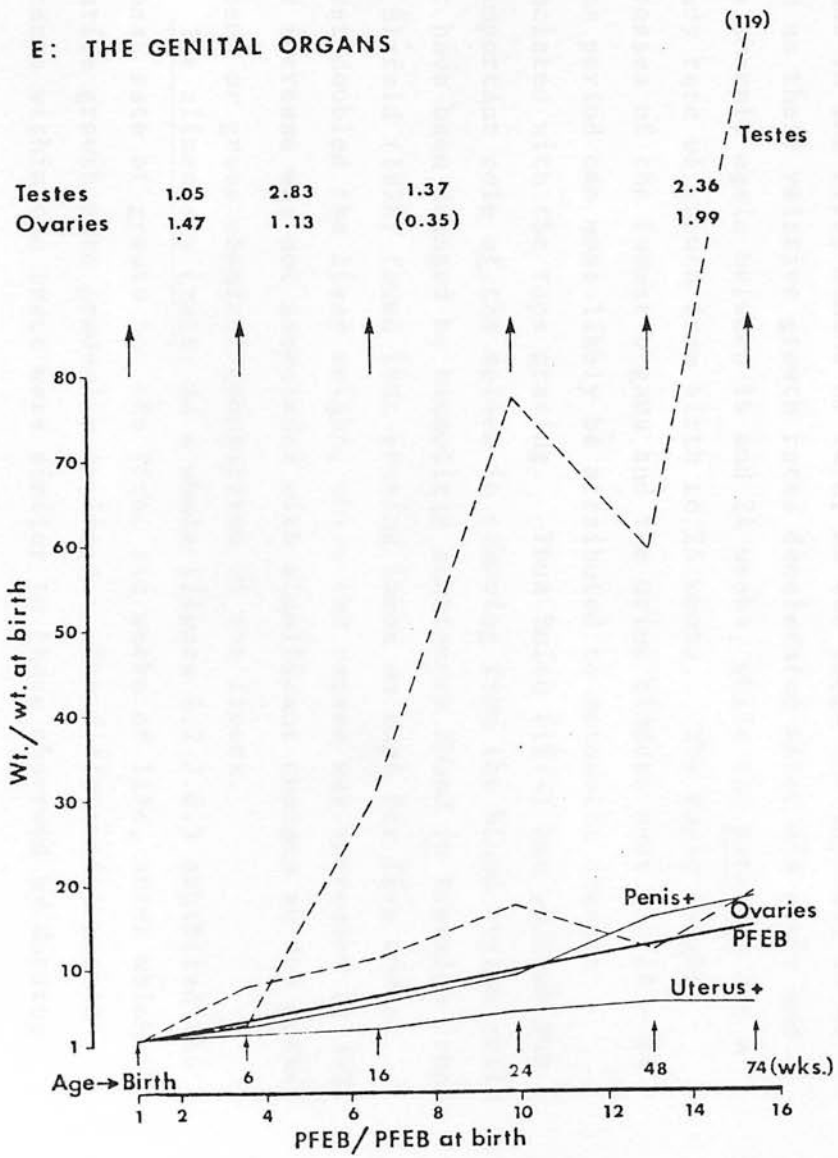
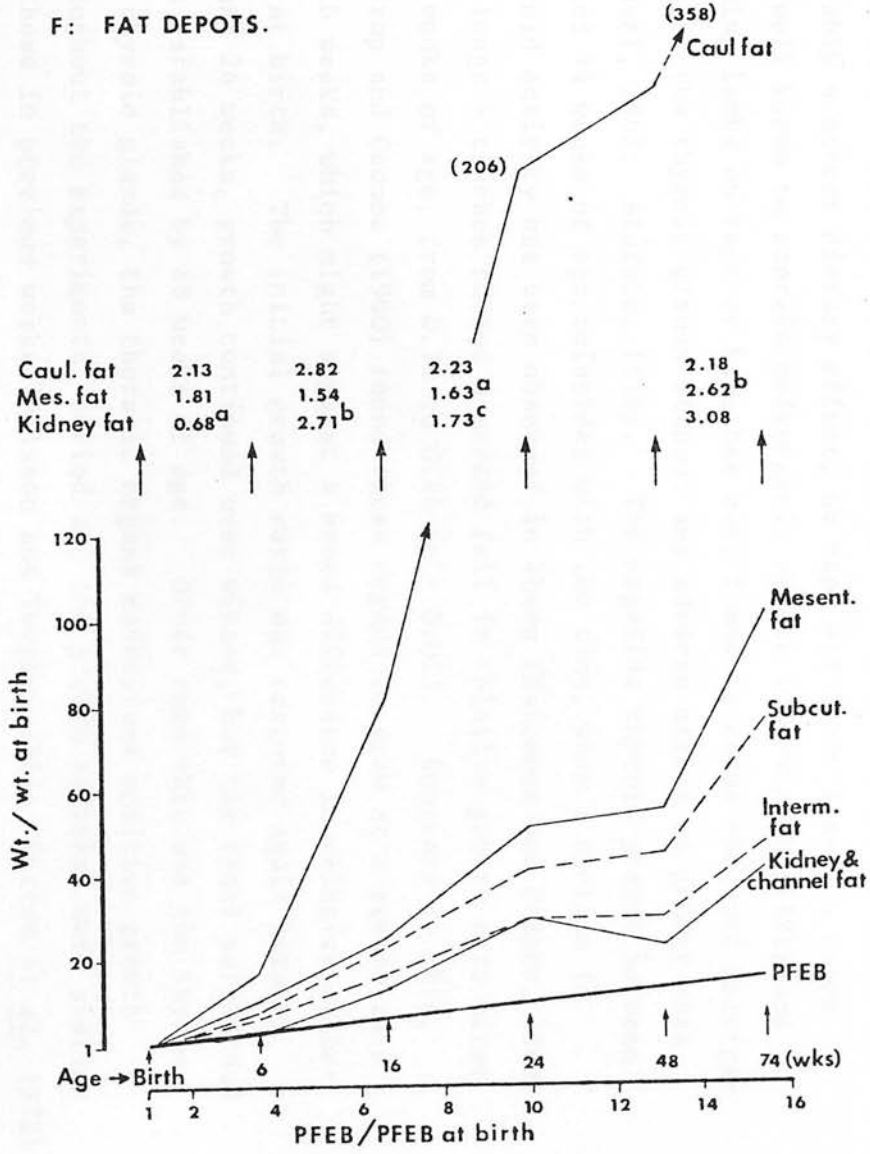


Fig. 4:2:3. Contd.





variable pattern of growth, the coefficient being 0.71 in the first interval, then falling to a non-significant value of 0.20 and rising again to 1.85 between 16 and 24 weeks. This sudden growth spurt was probably a direct dietary effect, as rape and other Brassica crops are well known to contain goitrogenic agents (Greenhalgh, 1971) and grazing lambs on rape or kale has been found to cause abnormal enlargement of the thyroid glands without any adverse effect on growth rate. (Russel, 1967; Bläfeld, 1976). The negative thyroid growth between 48 and 74 weeks of age coincides with the time, when a decline in thyroid activity has been observed in sheep (Falconer and Draper, 1968). The lungs + trachea showed a marked fall in relative growth rate after six weeks of age, from 0.70 to 0.46 ($p < 0.01$). Contrary to this, Wardrop and Coombe (1960) found these organs to grow at a steady rate to 16 weeks, which might suggest a breed difference in relative maturity at birth. The initial growth ratio was restored again between 16 and 24 weeks, growth continued over winter, but the final weight had been established by 48 weeks of age. Other than this and the thymus and thyroid glands, the thoracic organs maintained positive growth throughout the experimental period and the growth patterns were similar to those in previous works (Pålsson and Vergès, 1952; Kirton et al., 1972).

The liver, spleen and kidneys, (figure 4.2.3.c.) showed similar trends in the first months of life, as the lungs and thyroid, in as much as their relative growth rates decelerated after six weeks and rose sharply again between 16 and 24 weeks, while the pancreas had a steady rate of growth from birth to 24 weeks. The rapid weight increases of the former organs and the urine bladder over the 16 - 24 weeks period can most likely be attributed to metabolic changes associated with the rape grazing. Thus Smith (1974) has pointed out an important role of the spleen in removing from the blood stream cells that have been damaged by haemolitic substances found in Brassica crops, and Bläfeld (1976) found that grazing lambs on rape for five weeks almost doubled the liver weight, while the carass was increased by 30%. This increase was not associated with significant changes in dry matter content or gross chemical composition of the livers.

The alimentary tract, as a whole (figure 4.2.3.d.) exhibited the highest rate of growth for the first six weeks of life, after which the relative growth rate gradually declined. The differential growth patterns within the tract were similar to those observed by Wardrop

and Coombe (1960), the rumen showing the greatest and the oesophagus, abomasum and small intestine the least relative weight gain. The outstanding feature is the large weight increase of the caecum and the less marked increase of the colon + rectum over winter when the whole of the alimentary tract grew at a low rate. This can be attributed to roughage feeding, and similar distorting effects were found by Seebeck (1973a), on gut proportions in cattle, which were fed hay and straw to lose weight.

The genital organs (figure 4.2.3.e.) showed diverse patterns of development. The penis (+ retractor muscles + associated glands) and the uterus + vagina were steady in their relative growth rates, the former resembling that of the PFEB, while the latter grew at a lower rate and did not increase in weight beyond 48 weeks of age. The gonads exhibited a marked age and seasonal fluctuation. It is worth noting that the standard errors associated with the relative growth coefficients for these organs were considerably higher than for most other parts of the body, particularly after the earliest phase, thus indicating a poorer relationship with empty body weight. The ovaries had their period of highest relative growth rate between birth and six weeks and grew somewhat slower for the subsequent ten weeks period. While increasing their rate of growth again between 16 and 24 weeks, that gain was not significantly related to changes in empty body weight (b-value non-significant), indicating a dominating influence of other factors than body weight at that time. The ovaries had regressed by 48 weeks while regaining their previous peak weight by 74 weeks, which coincides with the time of year when daylight is rapidly falling in Iceland; this being known to influence sexual development in ewes (Dýrmundsson, 1973a). The testes initially grew at a relative rate similar to that of the empty body, while exhibiting a sharp rise in growth rate after six weeks of age, which is in accordance with earlier findings for a number of different breeds (Courot, 1962; Skinner, Booth, Rowson and Karg, 1968; Colyer, 1971). There is an apparent discrepancy regarding the decline in the relative growth coefficient between 16 and 24 weeks, coinciding with a rise in the slope of relative weight increase. This can only be explained by a limited degree of association between testes growth and empty body growth. While there appears to be little direct evidence for a relationship between photoperiodism and sexual development in ram lambs

(Dýrmundsson, 1973 b), such a relationship was suggested by Skinner and Rowson (1968) and could be a confounding factor in our data. Dýrmundsson (1978) found testes weight in Icelandic ram lambs to be more closely related to body weight (r = 0.65) than to age (r = 0.39). However, as all his measurements were recorded on the same day in the autumn, the variation in age arising through different dates of birth, the current data and his are not directly comparable. The regression of testes weight over winter and subsequent rapid weight increase, followed a common pattern observed in Icelandic rams (Dýrmundsson, personal communcation).

The internal fat depots (figure 4.2.3.f.) showed the commonly recognized order of development (Pálsson and Vergés, 1952; Kirton et al., 1972), caul fat growing fastest, followed by mesenteric fat, kidney fat and channel fat, in the respective order. There was an actual weight loss in the kidney + channel fat depots associated with the relatively slow winter growth, while caul fat and mesenteric fat still showed a marginal increase in absolute weight.

For comparative purposes, the two carcass fat depots are also included in figure 4.2.3.f. Relative to internal fat, these did not conform to the order demonstrated by earlier workers, eg. Pálsson and Vergés (1952) and Fourie (1965). The major discrepancy is seen in the development of subcutaneous fat, which in the current study was less advanced, both in absolute weight and relative to the other depots, than in either of the cited works. Thus, for instance, the ratio of subcutaneous fat to internal fat (including kidney fat) was 1.48 in the 41 week old high-plane wethers of Pálsson and Vergés (1952) and 1.37 in Fourie's (1965) 80 week old sheep, compared with 0.73 in the present 74 week old slaughter group. This comparison is most certainly confounded by different nutritional treatments as well as by different stages of development; however the markedly low ratio of subcutaneous fat to internal fat may well be a characteristic of the Icelandic breed of sheep, which until the turn of this century, was primarily kept for milk production. Such differences between beef and dairy breeds of cattle are commonly acknowledged (Pomeroy and Williams, 1974; Kempster, Cuthbertson and Harrington, 1976b; Williams, 1978).

b) Genotype effects.

Cannon line differences in relative growth coefficients, in the Edinburgh trial, were short of statistical significance, unsystematic

and would be difficult to interpret. There was no indication in this trial either of an interaction between cannon line and level of feeding, or actual daily intakes, with respect to relative growth rates or estimated weights of organs or parts at constant empty body weights.

In the Icelandic trial certain differences were observed between the two conformation types, although in most cases the relative coefficients were similar for both types. No interactions with sex or type of birth reached statistical significance. Those coefficients, which at some stage approached significant type differences, are presented in table 4.2.2. The greatest difference was observed for the thoracic organs in the first period, this being mainly due to the higher rates of the heart and lungs in the L-type. Differences, such as those for the head, liver and pancreas, should be interpreted with caution, as there might be negative correlations between growth coefficients over adjacent time intervals. Thus, for instance, if by chance the S-lambs killed at 16 weeks had lighter livers than the respective population, this would lower the growth coefficients for the preceding interval, while increasing the same value for the following period. An interesting difference was exhibited in the relative growth of caul fat. While both types showed the highest rate of growth between six and sixteen weeks, this rate was virtually maintained by the L-lambs for the succeeding eight weeks, whereas the S-lambs showed a marked fall in relative caul fat growth after 16 weeks of age. This might suggest an age-related difference in the rate of caul fat deposition, but it will be recalled from the last chapter, that the L-lambs grew slightly faster after weaning, which could have helped to sustain the higher rate of fat deposition.

Mean weights of the various body components have been estimated by log-log regressions, for two age intervals, at constant empty body weights and are presented in full in Appendix 8. Relative genotype differences for selected body components are shown in tables 4.2.3. and 4.2.4. for the Edinburgh and Icelandic trials, respectively.

There were few statistically significant differences between the Edinburgh cannon lines (table 4.2.3.) but more so on the feeding trial than before weaning, there being a greater number of lambs in the former estimates. When such differences existed, however, the control line lay intermediate to the L- and S-lines, indicating true selectional effects.

Table 4.2.2. Effect of conformation type on the relative growth rates (b) of selected body components[x].

(Iceland)

Component	Conf. type	0 - 6 wks.	SE	6 - 16 wks.	SE	16 - 24 wks.	SE
Carcass	L	1.07	0.018	0.94	0.036	1.08	0.065
	S	1.03	0.017	1.01	0.039	1.03	0.063
Head	L	0.62	0.021	0.83 *	0.027	0.79	0.129
	S	0.63	0.020	0.73	0.029	0.83	0.123
Feet	L	0.52	0.030	0.51	0.031	0.63	0.069
	S	0.46	0.028	0.46	0.033	0.63	0.065
Pelt	L	0.80 +	0.044	1.02	0.064	1.45	0.181
	S	0.67	0.041	1.04	0.068	1.44	0.171
Heart	L	0.92 *	0.049	0.82	0.602	0.80	0.141
	S	0.78	0.046	0.76	0.638	0.85	0.133
Lungs + trachea	L	0.75 +	0.035	0.52	0.072	0.86	0.188
	S	0.66	0.033	0.41	0.076	0.65	0.178
Tot. thoracic organs	L	0.90 **	0.022	0.67	0.057	0.90	0.156
	S	0.76	0.021	0.70	0.060	0.82	0.148
Liver	L	1.02	0.072	0.87 *	0.052	1.23	0.189
	S	1.09	0.067	0.66	0.055	1.40	0.179
Pancreas	L	1.22	0.077	1.25	0.133	0.88	0.235
	S	1.37	0.072	0.97	0.141	0.66	0.223
Omasum	L	1.66 +	0.110	2.15	0.160	(0.14)	0.395
	S	1.37	0.102	2.02	0.170	(0.43)	0.375
Caul fat	L	2.14	0.250	2.78	0.301	2.68 *	0.389
	S	2.12	0.233	2.86	0.319	1.79	0.369

x) Coefficients relating to PFEB, adjusted for sex and type of birth.

+) $p < 0.10$.

Table 4.2.3. Effect of cannon line on the weights of selected body components at constant pelt-free empty body weight (PFEB). (Edinburgh).

Component		Pre-trial: PFEB = 10 kg				On trial+: PFEB = 30 kg			
		Relat. diff. (C = 100)	Signific. of diff. L-C	L-S	C-S	Relat. diff. (C = 100)	Signific. of diff. L-C	L-S	C-S
Carcass	L	105	N.S.	N.S.	N.S.	100	N.S.	**	**
	S	104				104			
Head	L	98	N.S.	N.S.	N.S.	105	N.S.	N.S.	N.S.
	S	102				105			
Feet	L	108	N.S.	**	N.S.	107	**	**	**
	S	93				93			
Pelt	L	95	N.S.	N.S.	N.S.	96	N.S.	**	N.S.
	S	95				107			
Thoracic organs	L	99	N.S.	N.S.	N.S.	100	N.S.	N.S.	N.S.
	S	98				100			
Alimentary tract	L	85	*	N.S.	N.S.	101	N.S.	N.S.	N.S.
	S	98				100			
Liver	L	98	N.S.	N.S.	N.S.	95	N.S.	*	N.S.
	S	113				103			
Intestinal fat	L	-	-	-	-	79	**	**	N.S.
	S					101			
Kidney fat	L	87	N.S.	*	N.S.	84	**	N.S.	*
	S	119				85			

+) Adjusted to constant daily D.M. intake.

For absolute weights and standard errors see Appendix 8.

Table 4.2.4. Effect of conformation type on the weights of body components at constant pelt-free empty body weight (PFEB)+ (Iceland).

Component	PFEB = 15 kg		PFEB = 30 kg	
	Long/short (S = 100)	Signific. of diff.	Long/short (S = 100)	Signific. of diff.
Carcass	97	N.S.	96	**
Head	103	*	107	*
Feet	118	***	118	***
Pelt	103	N.S.	103	N.S.
Thoracic organs	117	***	112	**
Aliment. tract	107	N.S.	108	*
Liver	102	N.S.	99	N.S.
Testes	94	N.S.	103	N.S.
Penis + glands	98	N.S.	122	*
Ovaries	103	N.S.	116	N.S.
Uterus + vagina	125	N.S.	188	***
Intestinal fat	79	**	84	*
Kidney fat	60	***	68	***

+) Adjusted for sex and type of birth.
For absolute weights and standard errors see Appendix 8.

The notable exception was kidney fat, of which the C-lambs contained 18% more than either of the other lines ($p < 0.05$). It should also be noted, that the deviations of L- and S-lambs from the C-line were not always symmetrical. Thus the S-lambs had 4% higher proportion of carcass than the other two ($p < 0.01$), which were almost identical. Similarly, there was virtually no difference in intestinal fat weight between the S- and C-lines, while the L-lambs contained 21 - 22% less ($p < 0.01$). As would be expected, feet weight was positively related to cannon bone length, there being a 14% difference ($p < 0.01$) between the L- and S-lambs. No explanation will be offered for the apparent inverse relationships between the weights of the pelt and liver and cannon bone length. If anything, one would expect the leggier type of sheep to have a larger surface area, so the differences in pelt weight are likely to result from differences in skin thickness, wool quantity or in physiological properties of the pelt.

Table 4.2.4. shows several characteristic effects of conformation type in the Icelandic trial. The main effect has been to increase the proportions of carcass and internal fat depots in the empty body of the S-type, these differences being balanced by heavier head, feet and most thoracic and abdominal organs of the L-type. Relative differences were remarkably consistent at both points of estimation, although their magnitudes varied somewhat due to the previously discussed changes in relative growth rates. Thus, the difference in internal fat, in favour of S-lambs was reduced from 27% at 15 kg PFEB to 21% at 30 kg PFEB. The differences in pelt weight and liver weight, apparent between the Edinburgh-cannon lines, did not exist in the Icelandic trial. It is interesting to note, that the 8 - 11% difference in blood weight ($p < 0.05$-0.01), in favour of the L-lambs, was associated with a similar difference in heart weight. A functional relationship between the two would seem logical.

The L-lambs had heavier thyroids than the S-lambs, although this was significant only at early stages of growth. This feature is of particular interest in relation to conformational and compositional differences between the two types. Thus, Scow (1959) concluded from studies on rats, that thyroxin had a strong influence on the length growth and maturation of bones, while Lister (1976) cited several studies, which showed an inverse relationship between thyroid activity and fatness in pigs. Even if thyroid weight is a relatively poor

estimator of thyroid activity (Falconer and Draper, 1968), it is tempting to speculate that the observed difference in thyroid weight might bear some relation to the differences in fatness and skeletal development, which characterize the two conformation types. Similarly, the 14% heavier pancreas in the L-lambs at 30 kg PFEB ($p < 0.05$) might indicate a difference in metabolic activity.

It will be seen that the genital organs were better developed in L-lambs at 30 kg PFEB, the penis + associated glands weighing 22% more and the uterus + vagina almost twice that in the S-lambs. The ovaries were also heavier in L-lambs, although short of statistical significance. This difference was 16% estimated at 30 kg PFEB, but in the 24 weeks slaughter group the actual difference was 0.45 g (1.95 g - 1.50 g) or 30%. Both differences in the female had disappeared by 74 weeks of age and even at 48 weeks in case of the ovaries. These observations are of particular interest in relation to the reproductive performance of the dam flocks in their first year of life. The first difference between the two dam types, in this respect, was noticed at mating time when 11 of the S-ewes could not be treated with progestagen sponges, due to tightness of the vagina, compared with four L-ewes. Secondly, more S-ewes returned into oestrus after first mating (11 against 7), became barren (8 against 3) and none of them gave birth to twins, while four of the L-ewes did so. These features can most likely be ascribed to later sexual maturity in the S-type, as was indicated by the slower early growth of their genital organs. It would appear, however, that this apparent delay in sexual maturity had no effects on adult reproductive performance, as in later years the S-type has tended to be the more prolific type.

Not only did the L-type sheep contain a heavier alimentary tract, but the proportions of the various parts of the tract were also markedly different at 15 kg and 30 kg PFEB. Thus the relative differences were greatest for the oesophagus, omasum, small intestine and reticulum, in descending order of magnitude, while the other components were not significantly different in the two types. The heavier oesophagus in the L-type, might simply reflect a difference in length, there being a longer distance from the mouth to the rumen in these animals, while the other differences are more difficult to account for. They cannot be explained by one type being earlier maturing than the other, since they reflect no such order of development. It must be noted that, in the two oldest groups the pattern

was somewhat less consistent, but bearing in mind the great natural variation in the weight of these organs and the few animals killed at the later stages, the evidence is inconclusive.

Certain anologies can be drawn between the Edinburgh and Icelandic results. Thus the two selection procedures appear to have produced similar relative differences between the L- and S-lines/types with respect to the proportions of carcass, feet and intestinal fat (caul fat + mesenteric fat), at equal weights of the empty body, although the Edinburgh-cannon bone selection seemingly did not always cause equal responses in both directions. Such similarities were not, however, apparent for those internal organs that could be compared, but the fact that each breed was raised under entirely different conditions, might well be relevant in this respect. The Blackface lambs, on the whole, appeared to have heavier carcass, head, feet and pelt but lighter thoracic and digestive organs and less internal fat than the Icelandic lambs.

Comparing the Icelandic results with those of Kirton et al. (1972), striking similarities appear. Thus the L- and S-types in our work showed remarkably like differences, in most respects, as did the Romney and the Southdown. This gives support to the inevitable conclusion from the present results, that genetic selection, based on conformation, not only changes the external shape of the animal but also alters the relative proportions of various body parts and organs.

c) Influence of sex.

Relative growth coefficients for those body parts and organs, which at some stage approached significant sex differences, are presented in table 4.2.5. Such differences were most apparent during the first six weeks of life and none approached statistical significance between 16 and 24 weeks. There were, however, some indications of sex effects on relative growth rates between 48 and 74 weeks, although not presented here.

Proportional weights and relative sex differences are shown in table 4.2.6. estimated and presented in two different ways. As there was a vast difference in body weight between the sexes at 74 weeks, comparison on equal weight basis would be meaningless, hence only the weights as proportions of PFEB are presented for that

Table 4.2.5. Effect of sex on relative growth coefficients, relating body components to PFEB[x]. (Iceland).

Component	Sex	Age: 0-6 wks.			Age: 6-16 wks.		
				SE			SE
Head	M	0.68	**	0.022	0.86	**	0.026
	F	0.57		0.020	0.70		0.030
Spleen	M	1.15	*	0.078	0.43	N.S.	0.124
	F	1.48		0.071	0.27		0.142
Pancreas	M	1.18	*	0.078	0.94	+	0.128
	F	1.42		0.071	1.27		0.146
Heart	M	0.94	*	0.050	0.69	*	0.058
	F	0.76		0.045	0.88		0.066
Rumen	M	2.37	+	0.067	1.70	N.S.	0.076
	F	2.18		0.060	1.88		0.087
Abomasum	M	0.99	+	0.067	0.85	N.S.	0.133
	F	1.17		0.061	0.89		0.152
Caul fat	M	1.73	*	0.254	3.23	+	0.289
	F	2.53		0.230	2.42		0.331
Kidney fat	M	0.32	*	0.207	2.98	N.S.	0.234
	F	1.05		0.188	2.45		0.267
Channel fat	M	0.36	*	0.207	2.30	+	0.249
	F	1.07		0.187	1.57		0.284

x) Adjusted for conformation type and type of birth.

+) $p < 0.10$

Table 4.2.6. Effect of sex on the proportions of body components[+]. (Iceland).

Component	Sex	Males/Females (Female = 100)				Component weight as proportion of PFEB (PFEB = 100)				
		PFEB = 3.0 kg		PFEB = 30.0 kg		At birth Mean	SE		74 weeks Mean	SE
PFEB (kg)	M F					3.31 2.91	0.137 -		56.46 42.08	0.291 -
Carcass	M F	101	N.S.	97	*	55.9 54.5	1.22 -	*	59.9 61.7	0.60 -
Head	M F	102	N.S.	136	***	12.2 12.5	0.20 -	**	9.6 5.5	0.46 -
Feet	M F	103	N.S.	104	*	6.9 7.0	0.24 -	N.S.	2.0 2.0	0.05 -
Pelt	M F	102	N.S.	95	N.S.	14.7 14.8	0.78 -	N.S.	14.1 13.5	1.27 -
Blood	M F	96	N.S.	104	N.S.	7.2 7.8	0.26 -	*	3.7 4.5	0.15 -
Total thoracic organs	M F	105	N.S.	98	N.S.	4.8 4.6	0.07 -	**	2.4 2.8	0.05 -
Alimentary tract	M F	106	N.S.	105	N.S.	4.3 3.7	0.20 -	N.S.	6.6 7.4	0.27 -
Liver	M F	103	N.S.	98	N.S.	2.4 2.2	0.19 -	**	1.6 1.7	0.01 -
Spleen	M F	131	*	100	N.S.	0.18 0.13	0.013 -	*	0.11 0.15	0.012
Pancreas	M F	166	***	98	N.S.	0.15 0.09	0.011 -	N.S.	0.13 0.13	0.015 -
Thyroid	M F	160	*	87	N.S.	0.023 0.018	0.0031 -	N.S.	0.010 0.010	0.000 -
Heart	M F	95	N.S.	101	N.S.	0.89 0.91	0.061 -	N.S.	0.52 0.54	0.018 -
Lungs + trachea	M F	113	*	99	N.S.	2.7 2.5	0.13 -	N.S.	0.92 1.07	0.081 -

Table 4.2.6. (continued)

Component	Sex	PFEB = 3.0 kg		PFEB = 30.0 kg		At birth Mean		SE	74 weeks Mean		SE
Diaphragm	M	103	N.S.	93	*	0.56	N.S.	0.053	0.53	N.S.	0.022
	F					0.51		-	0.58		-
Kidneys	M	100	N.S.	104	N.S.	0.71	N.S.	0.061	0.23	N.S.	0.025
	F					0.63		-	0.25		-
Oesophagus	M	105	N.S.	94	N.S.	0.16	N.S.	0.007	0.15	N.S.	0.011
	F					0.15		-	0.16		-
Rumen	M	82	*	104	N.S.	0.30	N.S.	0.011	2.07	N.S.	0.105
	F					0.33		-	2.26		-
Reticulum	M	95	N.S.	106	N.S.	0.095	N.S.	0.012	0.32	N.S.	0.026
	F					0.090			0.35		-
Omasum	M	79	N.S.	103	N.S.	0.063	N.S.	0.007	0.24	N.S.	0.015
	F					0.070			0.24		-
Abomasum	M	128	*	96	N.S.	0.72	N.S.	0.052	0.55	N.S.	0.016
	F					0.55		-	0.55		-
Small intestine	M	109	N.S.	113	*	2.3	N.S.	0.17	1.72	N.S.	0.099
	F					2.0		-	1.84		-
Caecum	M	96	N.S.	109	N.S.	0.15	N.S.	0.007	0.36	N.S.	0.054
	F					0.14		-	0.52		-
Colon + rectum	M	97	N.S.	99	N.S.	0.50	N.S.	0.046	1.15	*	0.067
	F					0.47		-	1.52		-
Caul fat	M	123	N.S.	72	***	0.27	N.S.	0.062	4.72	N.S.	0.380
	F					0.16		-	6.02		-
Mesenteric fat	M	73	N.S.	75	***	0.37	N.S.	0.078	2.65	N.S.	0.211
	F					0.43		-	2.40		-
Kidney fat	M	104	N.S.	72	***	1.34	N.S.	0.111	2.45	N.S.	0.440
	F					1.20		-	3.90		-
Channel fat	M	150	N.S.	97	N.S.	0.32	N.S.	0.042	0.22	N.S.	0.090
	F					0.20		-	0.34		-

+) Adjusted for conformation type and type of birth.

group. It may indeed be argued that no comparison of males and females at constant empty body weight is biologically sound, as the males will always be physiologically younger and would therefore be expected to have less mature body proportions. However, such a comparison is of practical interest and, at any rate, early differences in body weight were small, and which ever method is used, does not alter the results to any great extent.

Pálsson (1955) stated that females generally attained a more advanced state of development in early life, while the males, as well as reaching greater ultimate size, would attain a higher degree of development at maturity than females. In the main, our results appear to support this view. Thus, when we compare the two sexes at equal PFEB, approximate of birth weight, we find that, as a rule, the earlier maturing parts and internal organs are heavier in the males. This is most clearly demonstrated within the alimentary tract, where the early maturing oesophagus, abomasum and small intestine were relatively heavier in males, while the reverse was true for the later maturing organs, especially the rumen, which we found to increase in weight more than any other digestive organ in post-natal life. The heart, which is known to grow at a fast rate early in foetal life (Wallace, 1948) and serves a vital function in the foetus was, however, similar in both sexes at birth. The weights of internal fat depots were very variable at this stage, but their relative growth rates were much higher in females immediately after birth. There was a tendency for reversal of that pattern after six weeks, indicating that the females entered their period of fastest fat growth earlier than males, while the latter eventually reached as high, if not higher, relative rates of internal fat deposition. This change in pattern was reflected by the difference in fat content, in favour of the females, being proportionately greater at 15 kg than at 30 kg PFEB. The pancreas, spleen and heart grew relatively faster in the males for the first six weeks, and the head showed a consistently higher relative growth rate to 16 weeks in males than in females, which is in keeping with earlier findings (Hammond, 1932; Pálsson and Vergés, 1952; Everitt and Jury, 1966a; Kirton et al, 1972).

The previously cited statement of Pálsson (1955) was based on the comparison of wethers and ewes by Pálsson and Vergés (1952), who found that, when continuously raised on a high plane of nutrition, the wethers

at 41 weeks had reached a higher degree of development of the carcass and abdominal fat depots, while the earlier maturing organs and the head comprised higher proportions of the empty body in ewes at that age. These differences were negligible in equally old but lighter sheep, which had been reared on a low plane of nutrition. Our oldest group showed the same feature in the development of organs, while the carcass and internal fat depots still comprised higher proportions of the empty body in the females, the difference being met by the heavier head and genital organs in the males. This apparent discrepancy can, however, be explained. Firstly, our males were entire, while those of Pålsson and Vergès were wethers, and our breed was horned, while theirs was the polled Suffolk x Halfbred cross. The superior masculine development of the head and horns, in our males, accounts for the vast sexual difference in the proportion of head in the oldest sheep. Secondly, it is clear that our feeding/grazing conditions, from 24 weeks onwards, did not support growth rates comparable with those in the cited work. Thus the potential, particularly for fat deposition in the carcass and body cavity, is likely to have been more depressed in males than females.

d) Influence of the type of birth.

Differences in body composition between singles and twins must be primarily nutritional in nature, the single born lambs enjoying a higher level of nutritional supply in foetal and early post-natal life, as is generally shown by heavier birth weights of these lambs and faster growth rates during the suckling phase.

Proportional weight differences between the two birth types, in the Icelandic trial, are presented in table 4.2.7. and relative growth coefficients for those parts or organs, which at some stage were close to showing significant birth type effects, are shown in table 4.2.8. In this study we were limited to the first five slaughter groups, since the lambs in the two oldest groups were all of the same birth type.

The difference in empty body weight was relatively greatest at birth, the singles being born 52% heavier than twins, while this difference had been reduced to 12% at 20 - 24 weeks of age. Thus, while the singles gained more weight, in absolute terms, specific growth rates were higher for the twins in post-natal life. Differences in body proportions were also greater at birth than at any later stage,

Table 4.2.7. Effect of type of birth on the proportions of the various body components[+]. (Iceland).

Component	Twins as % of singles at constant PFEB					
	PFEB = 3.0 kg		PFEB = 15.0 kg		PFEB = 30.0 kg	
Carcass	101	N.S.	92	***	95	*
Head	100	N.S.	(105	**)[x]	100	N.S.
Feet	86	**	91	***	93	***
Pelt	87	*	104	N.S.	102	N.S.
Blood	93	N.S.	104	N.S.	105	N.S.
Thoracic organs	81	***	87	***	103	N.S.
Alimentary tract	123	**	114	**	102	N.S.
Liver	67	**	100	N.S.	(124	***)[xx]
Spleen	81	N.S.	79	**	105	N.S.
Pancreas	74	*	119	*	113	N.S.
Thyroid	63	*	84	N.S.	(215	***)[xx]
Heart	91	N.S.	89	**	104	N.S.
Lung + trachea	73	***	87	**	94	N.S.
Diaphragm	95	N.S.	101	N.S.	95	N.S.
Kidneys	76	**	89	**	105	N.S.
Oesophagus	108	N.S.	108	N.S.	95	N.S.
Rumen	194	***	155	***	108	N.S.
Reticulum	156	*	135	***	99	N.S.
Omasum	125	*	157	***	103	N.S.
Abomasum	100	N.S.	112	N.S.	103	N.S.
Small intestine	118	N.S.	93	N.S.	86	N.S.
Caecum	141	**	132	**	(78	N.S.)[xx]
Colon + rectum	134	*	129	**	(71	*)[xx]
Caul fat	136	N.S.	111	N.S.	102	N.S.
Mesenteric fat	126	N.S.	107	N.S.	96	N.S.
Kidney + channel fat	100	N.S.	110	N.S.	100	N.S.

+) Adjusted for conformation type and sex.

x) Difference caused by two polled singles.

xx) All singles in 24 wks. group fed dry feed to slaughter, while all twins were killed off rape (see ch. 4.2.a.).

Table 4.2.8. Effects of type of birth on relative growth coefficients, relating body components to PFEB[x]. (Iceland)

Component	Birth type	Age: 0-6 wks. b		SE	Age: 6-16 wks. b		SE
Head	Single	0.62	N.S.	0.021	0.84	**	0.033
	Twin	0.63		0.021	0.72		0.025
Feet	Single	0.48	N.S.	0.030	0.44	+	0.038
	Twin	0.51		0.029	0.53		0.029
Liver	Single	0.89	**	0.073	0.70	N.S.	0.062
	Twin	1.23		0.070	0.83		0.047
Pancreas	Single	1.07	**	0.078	1.22	N.S.	0.159
	Twin	1.52		0.074	1.00		0.120
Thyroid	Single	0.44	*	0.127	(0.37)	N.S.	0.244
	Twin	0.98		0.122	(0.03)		0.185
Lungs	Single	0.61	**	0.035	0.44	N.S.	0.086
	Twin	0.80		0.034	0.49		0.065
Total thoracic organs	Single	0.80	+	0.022	0.64	N.S.	0.068
	Twin	0.87		0.021	0.72		0.052
Rumen	Single	2.26	N.S.	0.066	1.95	*	0.094
	Twin	2.29		0.063	1.63		0.072
Alimentary tract	Single	1.64	*	0.044	0.93	N.S.	0.083
	Twin	1.79		0.042	0.90		0.063

x) Adjusted for conformation type and sex.

+) $p < 0.10$

but here we have to make a clear distinction between comparison at constant PFEB, on the one hand, and that of unadjusted component weight as a proportion of PFEB, on the other. On the latter basis, the singles inevitably show more mature proportions at birth purely because of the difference in weight. Therefore, the comparison at equal empty body weight gives a clearer indication of true nutritional effects, provided that the mathematical procedure involved is sound. The values in table 4.2.7. have been obtained by log-log regressions of component weight on PFEB. The estimation of body composition at birth, necessitated the inclusion of the six weeks old slaughter group, as regressional analysis within the birth group alone would be unsafe, due to the narrow and non-overlapping weight ranges of the two types. The disadvantage of this approach is, that our estimation at an approximate birth weight, will to some extent be influenced by post-natal development. Since, however, there is no extrapolation, outwith the range of the data, the method is considered to be justified.

The various parts and organs in table 4.2.7. can be divided into three categories, according to their relative proportions in singles and twins at birth (PFEB = 3.0 kg): Those parts that were more retarded (values well below 100), similarly retarded (values around 100) and less retarded (values well above 100) than the empty bodies of twins. Most affected were the thyroids, liver, lungs, pancreas, kidneys and spleen ($p > 0.05$ for spleen), the feet and pelt also being significantly more affected than the empty body. The second category includes the carcass, head, blood, heart, diaphragm, oesophagus, abomasum, small intestine, kidney fat and channel fat, while the rumen, reticulum, omasum, caecum, large intestine, caul fat and mesenteric fat ($p > 0.05$ for fat depots) were least retarded in the twins and therefore appear heavier on a constant PFEB scale, although in fact all components were lighter in the twins.

With few exceptions, this pattern reflects the degree of maturity reached by the respective parts at birth, relative to the final weights at 74 weeks of age (figure 4.2.1. and 4.2.3.). Thus all the most retarded organs, except the pancreas, gained proportionately less weight post-partum than the empty body, while the least retarded digestive organs and fat depots represent the latest maturing components of the body. It must be noted, however, that the order of retardation,

for individual parts or organs, was not exactly the reverse of the order of relative post-natal weight gains. For instance, the liver was more retarded and the feet, head and heart somewhat less than such an order would predict.

Table 4.2.8. shows that the most retarded organs in the twins exhibited a marked recuperative capacity, in their immediate post-natal existence, by growing at relatively faster rates than the same organs in the singles. Thus, the initial differences gradually declined with increasing body weight, and most had disappeared at 30 kg PFEB. If the bracketed values are overlooked, these effects most likely being dietary ones, the only remaining significant differences at this stage were observed for carcass and feet weights. The difference in carcass weight was established in early post-natal life and was declining with age, while the feet appear to have been more permanently stunted in utero than any other component studied.

In comparing our findings with those of earlier workers, it is important that we are observing effects that arose through a different number of foetuses being carried by equally fed ewes, whereas most previous work has been concerned with various degrees of restricted maternal nutrition during gestation. The two effects may indeed not be the same. However, as we consider the differences between singles and twins to be primarily of nutritional origin, a view held also by Robinson and McDonald (1979), our findings are in direct conflict with those workers (Everitt, 1968; Fowler and Livingstone, 1972), who maintain that pre-natal undernutrition has a general rather than differential retarding effect on the foetus. We have adopted a similar mathematical approach to the problem as these workers, but nevertheless come to the conclusion that the effect is differential in nature, resulting in distorted weight proportions of the various body parts and organs at birth, which can not be simply explained by a difference in physiological age. This was the view established by the Cambridge School (Pálsson, 1955), which has recently gained support from experimental work at the Rowett Institute (McDonald, Wenham and Robinson, 1977; McDonald, Robinson, Fraser and Smart, 1979) as well as by the reanalysis of some earlier experiments by Robinson and McDonald (1979).

The pattern of retardation of the various body components, demonstrated in the present work, was not identical to that described by Wallace (1948) or Pálsson and Vergés (1952). The differences may, however, partly lie in the different mathematical approach. Thus,

Wallace found that, when plotted against foetal weight on a logarithmic scale, the liver, spleen and alimentary tract in the restricted lambs deviated from the 'normal' curve in the same fashion as we have observed. While other differences in Wallace's plots are less obvious, we have found a striking relationship between the degree of maturity, reached by the various components at birth, and the extent to which the same components were penalized by reduced foetal growth. Thus, in general, the organs that have been found, by present and previous workers, to be more advanced in development at birth than the rest of the body, were those that had been most retarded in the twinlambs, while the latest maturing organs had been least affected. This we can most easily interpret within the framework of the Cambridge ideas, namely that restricted nutrition over any age interval has the greatest retarding effects on those organs or parts which have their highest growth intensity at that age (Pålsson, 1955). In our case, this interval would begin at an undefined stage of gestation and reach beyond parturition.

Finally, it is evident that the higher specific growth rates of the twins, which were established soon after birth, and the somewhat higher absolute gains by the same lambs after nine - twelve weeks, were associated with the restoration of 'normal' weight proportions of most body parts and organs, except the feet, which at 30 kg empty body weight, still had not recovered from foetal retardation.

e) Summary.

1. The different body parts and organs were found to grow at vastly different rates, in post-natal life, relative to the empty body. The developmental pattern was in broad agreement with previous findings, the feet showing the least and caul fat the most proportionate weight increases of those parts studied.

2. Development of the body was characterized by changing, rather than constant differential growth ratios of most organs, making the application of Huxley's allometric equation unsafe over any extended interval of growth.

3. The major effect of reducing cannon bone length was to increase the proportions of carcass and internal fat depots in the empty body, whereas a longer cannon bone was associated with heavier feet and some internal organs.

4. Weight proportions of body components were different in the two sexes, but not in a constant fashion. Females showed a higher degree of development in early life, while there was some indication of this being reversed with higher age.

5. Substantial differences in body composition were demonstrated between singles and twins, most of which had been established by birth and gradually declined with age. The earlier maturing organs were found to be most retarded and the latest maturing organs least affected by the reduced foetal growth of twin lambs.

CHAPTER 5.

GROWTH AND DEVELOPMENT OF THE CARCASS

5.1. INTRODUCTION

Thanks to workers in the Hammond school and numerous later workers, the heterogenic nature of body development is now well documented. This was described by Pálsson (1955) as 'a primary wave of growth from the cranium down to the facial part of the head and backwards to the lumbar region. A secondary wave of growth starts from the lower parts of the limbs, down to the digits and upwards along the limbs and the trunk to the lumbar region, which is the last part of the body to attain its maximum growth rate and is consequently the latest maturing part of the animal'. Furthermore,'the different tissues also attain their maximum rate of growth in a definite order with age as follows: (1) nervous tissue, (2) bone, (3) muscle, and (4) fat. Moreover, fat is accumulated in the various depots with age at different rates in the following order of increasing rate: mesenteric fat, kidney fat, intermuscular fat and subcutaneous fat'. With minor modifications this pattern has since been verified by numerous workers, eg. in sheep Fourie (1965) and Wood, MacFie, Pomeroy and Twinn (1980); in cattle Berg and Butterfield (1968, 1976), Kempster, Cuthbertson and Harrington (1976a), Kempster, Avis and Smith (1976a) and Berg, Anderson and Liboriussen (1978a,b,c,d); in pigs Fowler and Livingstone (1972), Davies (1974a), Cole, White, Hardy and Carr (1976), Evans and Kempster (1979) and Kempster and Evans (1979). The major additional contribution to the theory of differential growth was the demonstration (Butterfield, 1963b; Fourie, 1965) that the lower abdominal region was later maturing than the upper lumbar region; a sequence that could not be detected by the original workers on account of their jointing technique, which did not differentiate between dorsal and ventral regions.

The consequence of this differential growth is a gradual change in carcass proportions as an animal approaches maturity. Thus the muscle; bone ratio increases with weight, while the proportions of both muscle and bone in the carcass fall due to the increasing rate of fat deposition (Prescott, 1979). Similarly, the extremities become relatively lighter and the thoracic-abdominal regions heavier, as carcass weight increases.

A desirable carcass type has already been described in general terms,

ie. one with a high percentage of lean and the more valuable cuts, optimal level of fatness, for the respective market, and the minimum of inedible tissue. The shape of individual joints is also of commercial interest, particularly in sheep, since the meat is commonly sold on the bone. Evidently, the composition and conformation of a carcass are closely related to the stage of development at slaughter. The controversial issue relating to the present study, concerns the possibility of the breeder to change his livestock through genetic selection in the desired direction. The school of thought, that maintains that carcass proportions and composition can be effectively improved by changing the external body form, has been challenged by many recent workers (Kirton and Pickering, 1967; Berg and Butterfield, 1976) and vast research has been conducted to evaluate differences between various breeds of livestock, representing widely different types of conformation. While the common view appears to be that breeding work has failed, to any important extent, to alter the distribution of lean tissue and bone within the carcass, there is no doubt that substantial breed differences exist with respect to muscle: bone ratio, total fat deposition, partition of fat between various depots and relative proportions of whole carcass joints. Reports demonstrating some or all of these effects include Fourie (1965), McClelland and Russel (1972), Weddell (1973), Wilson (1975), Boylan, Berger and Allen (1976), Kempster and Cuthbertson (1977), Wood et al. (1980) in sheep, Hankins Knapp and Phillips (1943), Callow (1961), Berg and Butterfield (1966), Broadbent, Ball and Dodsworth (1976), Berg, Andersen and Liboriussen (1978a) in cattle, and Davies (1974a) and Goenaga and Carden (1979) in pigs.

The beef breeds of cattle and improved mutton breeds of sheep have generally, although not invariably, been found to have thicker musculature, smaller skeletal frame, higher muscle: bone ratio and sometimes more subcutaneous relative to intermuscular fat than less improved breeds for meat production. Such characteristics were found, by some early workers (Hammond, 1932; Pálsson, 1939, 1940), to be associated with the length and shape of the fore cannon bone, this being shorter, more flat-shafted and with thinner extremeties in the conventional British mutton breeds, as compared with semi-wild or less improved sheep breeds. These and similar observations inspired the selection programmes which provided the sheep for the present study. While both Barton, Phillips and Clarke (1949) and Pálsson (1974) demonstrated that lambs

sired by short-legged rams gave blockier, higher grading carcasses with deeper 'eye - muscle' and smaller skeletal structure, our object is to examine how such differences in shape, within the same breed, relate to actual weight proportions of the major carcass joints and tissues.

The influence of sex on carcass composition is of interest in relation to the efficiency of meat production in general. It is acknowledged that males have a greater potential for lean tissue growth (Fowler, Taylor and Livingstone, 1969; Hammond, Jr., Mason and Robinson, 1971) which is related to their greater ultimate weight. Pálsson (1955) described sex differences in sheep in terms of earliness of maturity and stated that ewes would mature earlier than wethers which were earlier maturing than rams. When compared at equal age or weight, during the rapid growth phase, ewes have been found to contain more fat than wethers (Seebeck, 1966), which are fatter than entire rams (Bradford and Spurlock, 1964; Everitt and Jury, 1966b). Interactions between the plane of nutrition and the effects of sex or castration have been demonstrated by Pálsson and Vergés (1952) and Prescott (1969).

Fourie, Kirton and Jury (1970) demonstrated higher growth coefficients for muscle and bone, relative to carcass weight, in rams than in ewes. They also found ewes to have higher muscle: bone ratio than rams. The evidence regarding relative growth of muscle and bone is, however, uncertain (Field, 1971; Mukhoty and Berg, 1971).

Thus, it appears that sex affects carcass development particularly with respect to fat deposition relative to muscle and bone growth. Care must, however, be taken in the interpretation of results from various sources, because of the close association between tissue composition and stage of development, which is almost invariably different for the two sexes when compared at equal age or carcass weight.

5.2. RESULTS

The results from each trial have been presented in several ways: (1) as absolute and relative gains of carcass and carcass tissues, (2) as percentage tissue composition, and (3) as certain tissue ratios at constant carcass weights or ages.

a) Absolute gains.

Tables 5.2.1. and 5.2.2. show the absolute growth in weight of the carcass and its main constituent tissues for the Edinburgh feeding trial and the Icelandic study, respectively. Since the Edinburgh results were significantly influenced by daily D.M. intake and length of time on trial, values adjusted for these factors are also presented. After adjustment for intake and time, carcass and muscle gains were not significantly different for L- and S-lambs; however, the C-lambs gained 10% less per day in carcass weight and some 12% less in muscle content. Bone grew significantly faster in L-lambs than in either of the other lines ($p < 0.05 - 0.001$). Daily fat deposition was 10% greater in the S-lambs ($p < 0.05$) compared with either C- or L-lambs. On average, muscle, fat and bone comprised approximately 44%, 49% and 7% of carcass gain, respectively.

In the Icelandic sheep, (table 5.2.2., figure 5.2.1.), there was no significant difference between the L- and S-types in carcass gain or weight at any stage. Carcass gain was highest for the first six weeks, declined subsequently but accelerated again in the eight weeks period after weaning. Growth was slow over winter but somewhat faster during the second summer. While muscle initially comprised 59% of the gain, this had fallen to 47% between 16 and 24 weeks. At the same time the proportion of fat in the gain was increased from 17% to 40% while that of bone fell from 13% to 7%. Despite the slow gain in carcass weight during winter, bone showed an uninterrupted growth pattern, while fat deposition was virtually nil.

Although type differences in daily muscle gain were non-significant, total carcass muscle was 8.6% heavier ($p < 0.05$) in the L-type by 24 weeks of age. Bone growth was significantly faster in the L-type ($p < 0.001$), resulting in a 22.6% difference in carcass bone weight at 24 weeks ($p < 0.001$). The pattern of fat growth was also markedly different. The S-type showed a uniform increase in fat deposition throughout the first 24 weeks, while the L-type essentially maintained a constant rate up to weaning, after which fat was deposited at the same rate as in S-lambs. Consequently, the difference in fat content was greater at 16 weeks in favour of S-lambs, or 31% ($p < 0.01$) compared with 16% ($p < 0.05$) at 24 weeks.

Table 5.2.1. Effect of cannon line on carcass and tissue growth on the Edinburgh feeding trial.

Component	Line	Unadjusted					Adjusted+				
		Rate of gain (g/d)		Signific. level			Rate of gain (g/d)		Signific. level		
		Mean	SE	L-C	L-S	C-S	Mean	SE	L-C	L-S	C-S
Carcass++	L	79.1	2.69	*	N.S.	N.S.	82.6	2.04	N.S.	N.S.	*
	C	71.8	2.39				76.9	1.95			
	S	77.3	3.09				85.7	2.75			
Muscle	L	35.6	1.50	*	N.S.	N.S.	36.9	1.39	N.S.	N.S.	*
	C	30.8	1.32				33.2	1.33			
	S	35.0	1.72				38.4	1.88			
Bone	L	6.1	0.25	***	**	N.S.	6.3	0.24	***	*	N.S.
	C	4.4	0.22				4.6	0.23			
	S	4.8	0.28				5.3	0.33			
Fat	L	37.2	1.83	N.S.	N.S.	N.S.	40.4	1.07	N.S.	*	*
	C	36.6	1.62				40.7	1.07			
	S	38.5	2.10				44.7	1.44			

+) All means adjusted by regressions to 100 days on trial and to 800 g daily D.M. consumption.

++) Warm carcass, less kidney + channel fat.

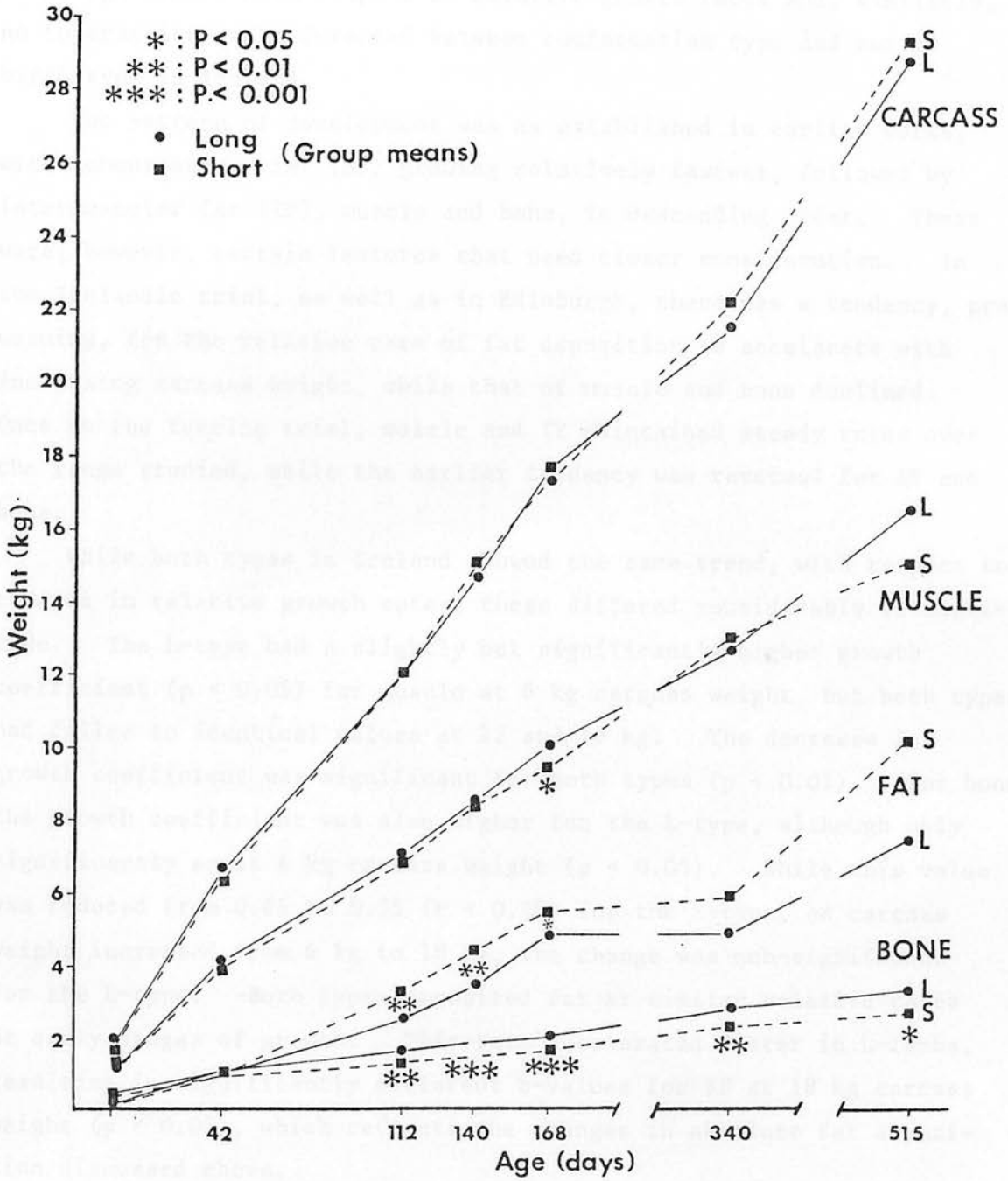
Table 5.2.2. Effect of conformation type on carcass and tissue growth from birth to 24 weeks[+]. (Iceland).

Component	Type	Daily gains (g/day)							
		Birth - 6 wks.		6 - 16 wks.		16 - 24 wks.		Birth - 24 wks.	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Carcass[++]	L	122	4.1	80	6.0	104	9.9	99	2.4
	S	117	-	85	-	98	-	97	-
		N.S.		N.S.		N.S.		N.S.	
Muscle	L	74.1	2.79	44.8	3.20	50.6	5.77	54.0	1.55
	S	68.5	-	42.4	-	44.5	-	49.6	-
		N.S.		N.S.		N.S.		N.S.	
Bone	L	15.5	0.66	8.3	0.86	7.6	1.10	9.9	0.18
	S	14.8	-	5.3	-	6.5	-	8.0	-
		N.S.		*		N.S.		***	
Fat	L	18.7	2.30	21.8	2.10	40.6	4.73	27.3	1.36
	S	20.9	-	32.1	-	40.0	-	31.9	-
		N.S.		**		N.S.		*	

+) Adjusted for year, sex and type of birth.

++) Warm carcass, less kidney + channel fat.

Figure 5:2:1. GROWTH OF THE CARCASS AND ITS TISSUES.
(ICELAND)



b) Relative tissue growth.

Relative growth coefficients, relating tissue growth to that of the carcass, are expressed in figures 5.2.2. and 5.2.3. Except for muscle and intermuscular fat on the Edinburgh feeding trial, all the coefficients had to be derived from quadratic equations. There were no significant line differences or line x intake interactions in the Edinburgh trial, with respect to relative growth rates and, similarly, no interactions were detected between conformation type and sex or birth type in Iceland.

The pattern of development was as established in earlier works, with subcutaneous fat (SF) growing relatively fastest, followed by intermuscular fat (IF), muscle and bone, in descending order. There were, however, certain features that need closer consideration. In the Icelandic trial, as well as in Edinburgh, there was a tendency, pre-weaning, for the relative rate of fat deposition to accelerate with increasing carcass weight, while that of muscle and bone declined. Once on the feeding trial, muscle and IF maintained steady rates over the range studied, while the earlier tendency was reversed for SF and bone.

While both types in Iceland showed the same trend, with respect to changes in relative growth rates, these differed considerably in magnitude. The L-type had a slightly but significantly higher growth coefficient ($p < 0.05$) for muscle at 6 kg carcass weight, but both types had fallen to identical values at 12 and 18 kg. The decrease in growth coefficient was significant for both types ($p < 0.01$). For bone, the growth coefficient was also higher for the L-type, although only significantly so at 6 kg carcass weight ($p < 0.05$). While this value was reduced from 0.66 to 0.55 ($P < 0.05$) for the S-type, as carcass weight increased from 6 kg to 18 kg, the change was non-significant for the L-type. Both types deposited fat at similar relative rates at early stages of growth. This rate accelerated faster in L-lambs, resulting in significantly different b-values for SF at 18 kg carcass weight ($p < 0.05$), which reflects the changes in absolute fat deposition discussed above.

While, in general, the two breeds of sheep in our work, have shown similar patterns of relative growth, with respect to SF, muscle and bone, this was not so in regard to IF which, on the Edinburgh feeding trial, showed a remarkably lower relative rate than in

Figure 5:2:2. RELATIVE GROWTH OF CARCASS TISSUES (EDINBURGH)

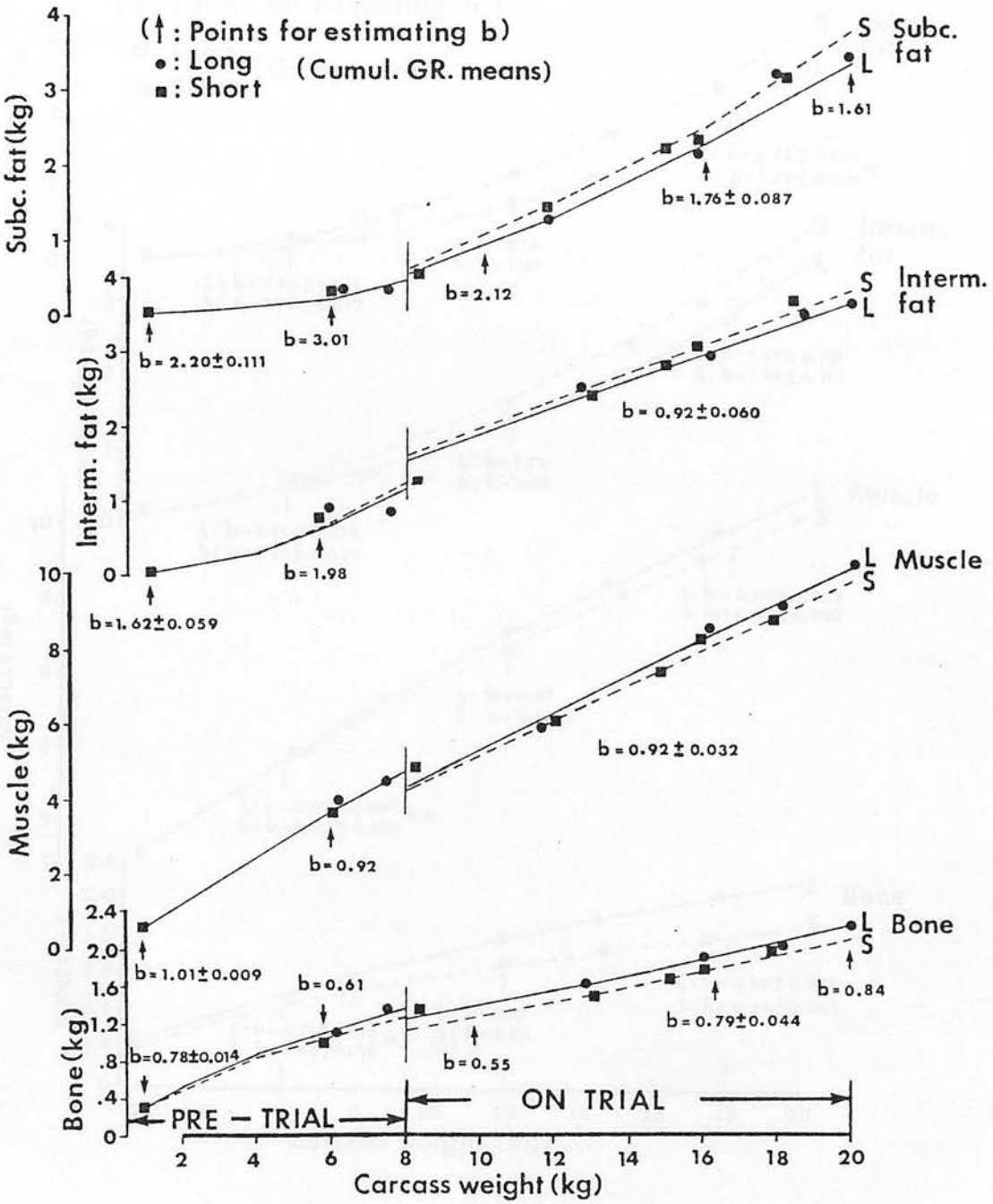
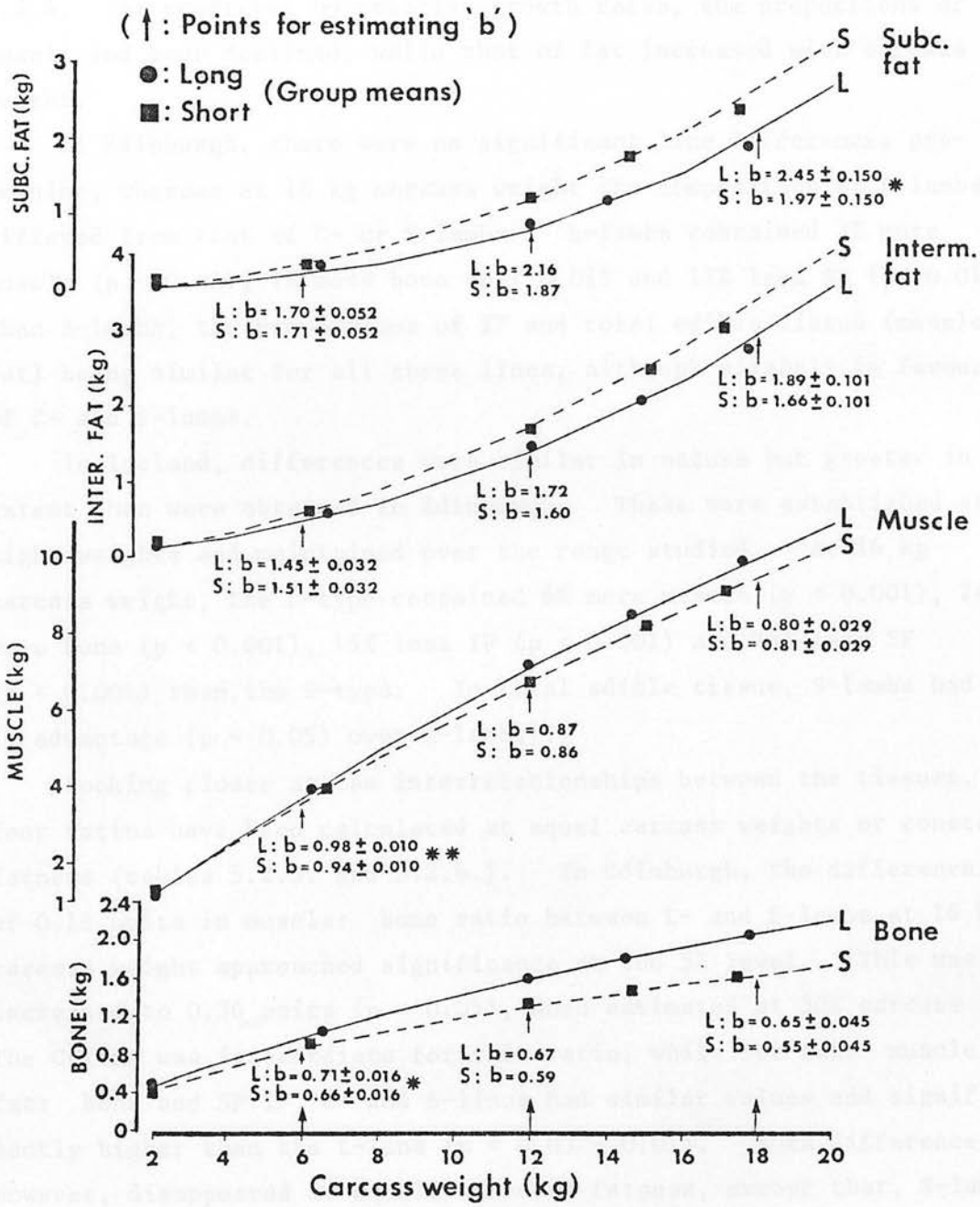


Figure 5:2:3. RELATIVE GROWTH OF CARCASS TISSUES (ICELAND) (64 lambs: Birth – 24 weeks)



Iceland. Although confused by different treatments, this may suggest different breed characteristics in the partitioning of carcass fat.

c) Carcass composition

Tissue weights have been estimated by log-log regressions (quadratic and/or linear) and are expressed in tables 5.2.3. and 5.2.4. As predicted by relative growth rates, the proportions of muscle and bone declined, while that of fat increased with carcass weight.

In Edinburgh, there were no significant line differences pre-weaning, whereas at 16 kg carcass weight the composition of L-lambs differed from that of C- or S-lambs. L-lambs contained 3% more muscle ($p < 0.05$), 7% more bone ($p < 0.01$) and 11% less SF ($p < 0.01$) than S-lambs, the proportions of IF and total edible tissue (muscle + fat) being similar for all three lines, although slightly in favour of C- and S-lambs.

In Iceland, differences were similar in nature but greater in extent than were observed in Edinburgh. These were established at light weights and maintained over the range studied. At 16 kg carcass weight, the L-type contained 6% more muscle ($p < 0.001$), 24% more bone ($p < 0.001$), 15% less IF ($p < 0.001$) and 25% less SF ($P < 0.001$) than the S-type. In total edible tissue, S-lambs had a 3% advantage ($p < 0.05$) over L-lambs).

Looking closer at the interrelationships between the tissues, four ratios have been calculated at equal carcass weights or constant fatness (tables 5.2.5. and 5.2.6.). In Edinburgh, the difference of 0.16 units in muscle: bone ratio between L- and S-lambs at 16 kg carcass weight approached significance at the 5% level. This was increased to 0.36 units ($p < 0.05$), when estimated at 30% carcass fat. The C-line was intermediate for this ratio, while for fat: muscle, fat: bone and SF:IF, C- and S-lines had similar values and significantly higher than the L-line ($p < 0.05 - 0.01$). Such differences, however, disappeared at equal degree of fatness, except that, S-lambs still had a higher proportion of fat relative to bone than L-lambs ($p < 0.05$).

In Iceland, type differences were greater and more consistent. The S-type had 0.4 - 0.8 units higher muscle: bone ratio ($p < 0.001$)

Table 5.2.3. Effect of cannon line on carcass composition [+]. (Edinburgh)

Tissue	Line	Pre-trial: Carcass = 8.0 kg				On trial: Carcass 16.0 kg [++]					
		Wt. (g)		% of	Relat. diff.	Wt. (g)		% of	Relat. diff.	Signific. level	
		Mean	SE	Carcass	(C = 100)	Mean	SE	Carcass	(C = 100)	L-C	L-S	C-S
Muscle	L	4856	76	60.7	100	8304	80	51.9	104			
	C	4859	80	60.7		7984	72	49.9		**	*	N.S.
	S	4904	88	61.3	101	8046	94	50.3	101			
Bone	L	1352	44	16.9	101	1904	22	11.9	106			
	C	1344	44	16.8		1796	20	11.2		**	**	N.S.
	S	1280	48	16.0	96	1776	24	11.1	99			
Inter-muscular fat	L	784	60	9.8	95	2980	52	18.6	96			
	C	824	60	10.3		3110	52	19.4		N.S.	N.S.	N.S.
	S	776	72	9.7	94	3122	68	19.5	100			
Subcu-taneous fat	L	160	24	2.0	83	2338	54	14.6	88			
	C	192	28	2.4		2654	56	16.6		**	**	N.S.
	S	208	28	2.6	108	2632	72	16.5	99			
Total carcass fat	L	944	40	11.8	93	5324	52	33.3	92			
	C	1016	44	12.7		5766	54	36.0		**	**	N.S.
	S	984	52	12.3	97	5740	70	35.9	100			
Muscle + fat	L	5800	43	72.5	99	13628	48	85.2	99			
	C	5875	46	73.4		13750	45	85.9		N.S.	N.S.	N.S.
	S	5888	51	73.6	100	13786	59	86.2	100			

+) Estimated by regressions for half carcass.

++) Adjusted to 800 g daily D.M. consumption.

All pre-trial differences non-significant.

Table 5.2.4. Effect of conformation type on carcass composition+. (Iceland).

Tissue	Type	Carcass = 8.0 kg				Carcass = 16.0 kg			
		Wt. (g) Mean	SE	% of Carcass	Relat. diff. (S = 100)	Signific. level	Wt. (g) Mean	SE	% of Carcass	Relat. diff. (S = 100)	Signific. level
Muscle	L	5042	60	63.0	105	**	9236	86	58.0	106	***
	S	4792	56	59.9			8738	82	54.6		
Bone	L	1216	22	15.2	117	***	1948	28	12.2	124	***
	S	1038	18	13.0			1572	22	9.8		
Intramus-cular fat	L	742	28	9.3	79	***	2396	70	15.0	85	***
	S	934	34	11.7			2826	82	17.7		
Subcu-taneous fat	L	368	22	4.6	62	***	1596	74	10.0	75	***
	S	592	36	7.4			2136	100	13.4		
Total carcass fat	L	1114	46	13.9	73	***	3996	130	25.0	80	***
	S	1536	64	19.2			4966	162	31.0		
Muscle + fat	L	6156	38	76.9	97	**	13232	78	83.0	97	**
	S	6328	43	79.1			13704	91	85.6		

+) Estimated by regressions for half carcass; based on 64 lambs (birth - 24 wks.) and adjusted for sex and type of birth.

Table 5.2.5. Effect of cannon line on tissue ratios in the carcass[+]. (Edinburgh).

Tissue	Line	Carcass = 16.0 kg					Carcass fatness = 30%				
		Ratio	SE	Signific. level L-C	L-S	C-S	Ratio	SE	Signific. level L-C	L-S	C-S
Muscle: Bone	L	4.36	0.070				4.31	0.090			
	C	4.47	0.062	N.S.	N.S.	N.S.	4.46	0.104	N.S.	*	N.S.
	S	4.52	0.083				4.67	0.142			
Fat: Bone	L	2.85	0.075				2.40	0.035			
	C	3.21	0.074	**	**	N.S.	2.43	0.043	N.S.	*	N.S.
	S	3.24	0.099				2.51	0.050			
Fat: Muscle	L	0.64	0.016				0.56	0.004			
	C	0.72	0.018	**	*	N.S.	0.55	0.004	N.S.	N.S.	N.S.
	S	0.71	0.024				0.55	0.005			
Subc. fat: Interm. fat	L	0.77	0.016				0.72	0.025			
	C	0.85	0.017	**	*	N.S.	0.69	0.029	N.S.	N.S.	N.S.
	S	0.82	0.023				0.74	0.036			

+) Estimated by regressions and adjusted for daily D.M. consumption.

Table 5.2.6. Effect of conformation type on tissue ratios in the carcass[+]. (Iceland).

A: At equal carcass weights (64 lambs: birth - 24 weeks).

Tissues	C. type	Carcass = 8.0 kg			Carcass = 16.0 kg		
		Ratio	SE	Signific. level	Ratio	SE	Signific. level
Muscle: Bone	L	4.14	0.078	***	4.74	0.071	***
	S	4.61	0.088		5.56	0.084	
Fat: Bone	L	0.92	0.047	***	2.05	0.084	***
	S	1.48	0.076		3.16	0.130	
Fat: Muscle	L	0.22	0.011	***	0.43	0.017	***
	S	0.32	0.016		0.57	0.023	
Subc. fat: Interm. fat	L	0.50	0.022	***	0.67	0.023	*
	S	0.64	0.028		0.77	0.027	

B: At equal (percentage) fatness (48 lambs: 16 - 24 weeks).

Tissues	C. type	Carc. fatness = 20%			Carc. fatness = 30%		
		Ratio	SE	Signific. level	Ratio	SE	Signific. level
Muscle: Bone	L	4.55	0.112	**	4.79	0.113	***
	S	5.16	0.202		5.38	0.079	
Fat: Bone	L	1.49	0.031	*	2.60	0.052	***
	S	1.63	0.054		2.94	0.037	
Fat: Muscle	L	0.33	0.003	*	0.54	0.004	N.S.
	S	0.32	0.004		0.55	0.003	
Subc. fat: Interm. fat	L	0.57	0.027	N.S.	0.67	0.031	*
	S	0.58	0.047		0.77	0.020	
Carcass wt. (kg)	L	13.15	0.594	**	18.16	0.780	**
	S	9.80	0.700		15.00	0.400	

+) Estimated by regressions and adjusted for sex and type of birth.

than the L-type, depending on the stage of development and basis for comparison. Similarly, at constant carcass weight, all the other ratios were significantly higher in the S-type ($p < 0.05 - 0.001$). At equal degrees of fatness, S-lambs maintained higher muscle: bone and fat: bone ratios ($p < 0.05 - 0.001$), while the relative amounts of fat and muscle were now very similar. The type of conformation showed an interaction with level of fatness, with respect to the SF:IF ratio. While there was no difference at 20% fatness, the S-type had significantly more SF relative to IF, or 15% ($p < 0.05$) at 30% carcass fat.

Comparing the two sets of data, while there were relatively small differences in composition, at early stages of development, these became more apparent as growth advanced. As before, one must be aware of the entirely different experimental conditions, when evaluating these apparent breed differences. Most outstanding was the higher proportion of muscle and lower proportion of fat at 16 kg carcass weight in the Icelandic lambs, the differences being on average 5.5 and 6.6 percentage units, respectively. It is also apparent that the muscle: bone ratio was higher in Iceland, while other tissue ratios were not markedly different at the same level of carcass fatness. It is important in this respect, that weight loss from slaughter to dissection was considerably higher in the Edinburgh trial (7.2%, compared to 3.4% in Iceland). Assuming that this is primarily moisture loss, most of which would come from the musculature (Tempest, 1976), the proportion of muscle, in relation to the carcass or any other tissue, will have been reduced to a greater extent in Edinburgh than in Iceland. As, however, moisture loss was uniform over the different lines or types in each trial, no attempt has been made to correct for this factor.

d) Relative growth of carcass joints and comparison of joint proportions.

Differences in relative growth rates of joints between cannon lines or conformation types were only slight and non-significant; hence the overall coefficients are presented in tables 5.2.7.a,b.

Considering the different anatomical divisions, the values are remarkably similar for both trials. As expected, the extremities showed the lowest and the flanks the highest relative growth rates, which partly results from the different proportions of bone and fat in these joints. The whole shoulder joint grew significantly slower than the carcass ($p < 0.001$), while the growth coefficients for

Table 5.2.7. Relative growth coefficients, relating joints to carcass weight.

A: Edinburgh

Joint	Pre-trial b	SE	Diff.	On trial+ b	SE
Prime shoulder + breast	0.96	0.006	-	0.96	0.019
Neck	0.84	0.021	-	0.83	0.048
Shank	0.74	0.018	**	0.57	0.045
Total rib	1.13	0.016	-	1.19	0.032
Prime loin				1.19	0.046
Loin flank				1.31	0.117
Total gigot	1.03	0.008	**	0.96	0.021

+) Adjusted for daily D.M. intake.

B: Iceland - Adjusted for conformation type, sex and type of birth.

Joint	b	SE
Total shoulder	0.93	0.004
Total rib	1.16	0.007
Prime loin	1.10	0.018
Loin flank	1.46	0.053
Prime gigot	0.88	0.013
Gigot flank	1.37	0.047

Table 5.2.8 Effect of cannon line on joint proportions of the carcass[+]. (Edinburgh).

Joint	Line	Pre-trial: Carcass = 8.0 kg				On trial: Carcass = 16.0 kg[++]					
		Wt. (g)		% of	Relat. diff.	Wt. (g)		% of	Relat. diff.	Signific. level	
		Mean	SE	Carcass	(C = 100)	Mean	SE	Carcass	(C = 100)	L-C	L-S	C-S
Prime shoulder + breast	L	2944	32	36.8	100	5468	30	34.2	101			
	C	2942	32	36.8		5406	28	33.8		N.S.	N.S.	N.S.
	S	2944	36	36.8	100	5460	38	34.1	101			
Neck	L	304	9	3.9	109	534	8	3.3	100			
	C	280	9	3.5		536	8	3.4		N.S.	N.S.	N.S.
	S	278	9	3.5	99	556	10	3.5	104			
Shank	L	294[a]	8	3.6	108	382	6	2.4	109			
	C	272[b]	8	3.4		352	4	2.2		**	**	N.S.
	S	256[b]	8	3.1	94	344	6	2.1	98			
Rib	L	968	20	12.1	100	2290	22	14.3	98			
	C	968	24	12.1		2340	22	14.6		N.S.	N.S.	N.S.
	S	1018	28	12.6	105	2348	28	14.7	100			
Prime loin[x]	L					1706	24	10.7	92			
	C					1858	24	11.6		**	**	N.S.
	S					1878	32	11.7	100			
Loin flank[x]	L					372	12	2.3	96			
	C					388	12	2.4		N.S.	*	*
	S					430	18	2.7	111			
Gigot	L	2816[a]	40	35.2	100	5444	34	34.0	102			
	C	2824[a]	40	35.3		5326	30	33.3		*	**	**
	S	2696[b]	44	33.7	95	5156	40	32.2	97			

+) Estimated by regressions for half carcass.

++) Adjusted for daily D.M. consumption.

x) Not separated in birth group.

Table 5.2.9. Effect of conformation type on joint proportions of the carcass[+]. (Iceland).

Joint	Type	Carcass = 8.0 kg				Carcass = 16.0 kg			
		Wt. (g) Mean	SE	% of Carcass	Relat. diff. (S = 100)	Signific. level	Wt. (g) Mean	SE	% of Carcass	Relat. diff. (S = 100)	Signific. level
Shoulder	L	3278	22	41.0	106	***	6362	34	39.8	105	***
	S	3086	20	38.6			6054	32	37.8		
Rib	L	1066	8	13.3	94	***	2374	22	14.8	93	***
	S	1138	8	14.2			2558	24	16.0		
Prime loin	L	638	10	8.0	91	**	1356	14	8.5	89	***
	S	700	12	8.8			1524	16	9.5		
Loin flank	L	196	12	2.5	82	*	498	16	3.1	77	***
	S	240	16	3.0			646	10	4.0		
Prime gigot	L	2722	28	34.0	103	*	5012	20	31.3	104	**
	S	2634	26	32.9			4822	19	30.1		
Gigot flank	L	186	10	2.3	89	N.S.	498	14	3.1	94	N.S.
	S	208	12	2.6			526	16	3.3		

+) Estimated by regressions for half carcass; based on 64 lambs (birth - 24 wks) and adjusted for sex and type of birth.

the rib and prime loin joints were greater than unity ($p < 0.001$). The Edinburgh data showed a significant decline in relative growth rates of the shank and gigot with time ($p < 0.01$). Similar trends were observed in Iceland for the whole shoulder and prime gigot, but to a lesser degree.

Despite the similarities in relative growth rates, there were significant line and type differences in joint proportions at constant carcass weights, as shown in tables 5.2.8. and 5.2.9. In Edinburgh, these differences were most marked when estimated after weaning. L-lambs were 11% heavier in the shank ($p < 0.01$), 5% in the gigot ($p < 0.01$), while being 9% ($p < 0.01$) and 13% ($p < 0.05$) lighter in the prime loin and loin flank, respectively, than the S-lambs. Controls were intermediate or close to the S-line. Similar effects were observed in Iceland, where the L-type had 5% heavier shoulder ($p < 0.001$), 4% heavier gigot ($p < 0.01$), but 8%, 12% and 30% lighter rib, prime loin and loin flank, respectively ($p < 0.001$), at 16 kg carcass weight.

There is an obvious association between line or type effects on joint proportions and the order of development of the respective joints, which can also be extended to the previously discussed differences in tissue composition. Thus, at constant weight, the magnitude of these differences grossly reflects the order of relative growth rates, the later developing joints or tissues being more advanced in S-lambs than in L-lambs; hence the former type can be described as being earlier maturing.

e) The development of carcass shape.

The relative growth coefficients presented in table 5.2.10. are indicative of the changes in carcass shape which are simultaneous with an increase in weight. Both the experiments revealed the same commonly acknowledged pattern of a relatively greater increase in width of the carcass than in either length or depth. Thus, with advancing development, the carcass attains a more compact form, as is best illustrated by plate 5.1. The different measurements reflect/a to varying degree the development of each tissue; hence it is not surprising that those measurements most indicative of the skeletal frame should show the lowest rate of increase.

Table 5.2.10. The development of carcass shape and the effect of cannon line or conformation type.

A: Edinburgh

Measurement	Pre-trial b^+	SE	On trial b^+	SE	Signific. of diff.	L-line as % of S-line at 16 kg carc.wt.	
Leg length (T)	0.22	0.013	0.25	0.026	N.S.	111	***
Depth of crutch (F)	0.18	0.015	0.27	0.039	N.S.	117	***
Width of gigots (G)	0.45	0.014	0.35	0.036	*	101	N.S.
Depth of thorax (Th)	0.36	0.011	0.26	0.013	***	104	**
Width of thorax (V)	0.39	0.012	0.45	0.022	N.S.	102	N.S.
Carcass length (L)	0.34	0.009	0.26	0.017	**	101	N.S.
L. dorsi length (A)	0.43	0.021	0.28	0.046	*	101	N.S.
L. dorsi depth (B)	0.47	0.027	0.16	0.073	**	91	*
Fat over L. dorsi (C)			1.82	0.159	-	95	N.S.
Fat on side (J)			1.46	0.145	-	97	N.S.

B: Iceland

Measurement	Birth-16 wks b^+	SE	16 - 74 wks b^+	SE	Signific. of diff.	L-type as % of S-type at 16 kg carc.wt.	
T	0.21	0.007	0.25	0.039	N.S.	113	***
F	0.15	0.010	0.19	0.056	N.S.	119	***
G	0.40	0.011	0.29	0.044	*	98	*
Th	0.34	0.006	0.29	0.031	N.S.	108	***
V	0.45	0.010	0.40	0.052	N.S.	92	***
L	0.35	0.006	0.24	0.033	**	107	***
A	0.35	0.014	0.37	0.061	N.S.	103	**
B	0.38	0.023	0.36	0.129	N.S.	86	***
C	1.59	0.177	1.57	0.637	N.S.	69	**
J	2.08	0.118	1.29	0.374	N.S.	64	***

+) Relative growth coefficients, relating to carcass wt.

For absolute line/type effects - see Appendix 9.

Comparison of the different genotypes revealed the differences in form which had been observed on the live animals. The Edinburgh cannon lines differed mostly in the length of the leg, there being only small differences in the trunk measurements, whereas in Iceland, the longer leg of the L-type was associated with a significantly longer and narrower trunk and a deeper thorax than of the S-type. These different features are of particular interest in relation to later discussion of tissue distribution.

The difference between measurements F and T (F-T), as well as the ratio of G/T are indicative of 'fleshiness' of the leg, i.e. thickness of flesh relative to length, and both these indices were strongly associated with a short cannon bone. Similarly, the S-line/type were superior with respect to the thickness and the cross-sectional area of the longissimus dorsi muscle, both of which are highly important characteristics in quality meat production. The differences in thickness were 2.6 mm and 3.7 mm at 16 kg carcass weight between the long and short lines and types, respectively. While the line differences in Edinburgh, regarding fat thickness, were non-significant, the S-type in Iceland had a thicker fat-layer over the l. dorsi (3.9 mm versus 2.7 mm) and on the side (10.2 mm versus 6.5 mm) at 16 kg carcass weight. However, the rate of increase in fat thickness, at that stage, was higher in the L-type, and the two types became more alike as weight increased.

f) Influence of sex on carcass development.

The two sexes did not differ markedly in relative growth rates of tissues or joints over the first 24 weeks of life, for which period growth coefficients were calculated. The data, however, indicates that such differences did exist at later stages of growth.

Proportions of joints and tissues in the carcass, as well as muscle: bone ratios, for each sex are presented in table 5.2.11. These have been analysed within slaughter groups, not to be confused with constant carcass weight, the 20 and 24 weeks groups being combined to give a more accurate estimate at that age.

It is evident that sex effects were generally small at birth, the only significant difference then being in the proportion of shoulder ($p < 0.05$), which was marginally higher in males. At 20 - 24 weeks the influence of sex had become more generally

Table 5.2.11. Effect of sex on carcass proportions and composition+. (Iceland).

Component	Sex	At birth			20 - 24 wks.			74 wks.		
		% of carcass			% of carcass			% of carcass		
		Mean		SE	Mean		SE	Mean		SE
Carcass (kg)	M	1.85	N.S.	0.109	16.54	N.S.	0.275	33.05	*	1.733
	F	1.58		-	15.84		-	25.37		-
Shoulder	M	45.6	*	0.24	40.0	***	0.22	42.7	**	0.53
	F	44.7		-	38.1		-	38.4		-
Rib	M	10.7	N.S.	0.38	15.2	*	0.16	16.1	N.S.	0.30
	F	10.6		-	15.7		-	16.5		-
Prime loin	M	7.9x	N.S.	0.12	8.7	***	0.08	8.3	N.S.	0.25
	F	8.0x		-	9.1		-	8.9		-
Loin flank	M				3.5	N.S.	0.07	3.2	N.S.	0.16
	F				3.6		-	3.6		-
Prime gigot	M	37.0x	N.S.	0.86	30.2	**	0.27	27.1	**	0.25
	F	38.5x		-	31.2		-	29.1		-
Gigot flank	M				3.2	N.S.	0.06	3.0	N.S.	0.25
	F				3.1		-	3.3		-
Muscle	M	60.2	N.S.	1.02	56.7	N.S.	0.62	55.4	N.S.	1.13
	F	60.4		-	55.7		-	53.0		-
Bone	M	21.9	N.S.	0.77	11.3	N.S.	0.13	10.9	*	0.30
	F	23.5		-	11.0		-	9.4		-
Interm. fat	M	6.6	N.S.	0.80	15.8	*	0.34	16.6	N.S.	0.66
	F	6.6		-	16.7		-	17.4		-
Subcut. fat	M	3.3	N.S.	0.21	10.8	*	0.42	12.2	N.S.	1.05
	F	3.1		-	12.1		-	15.0		-
Total carcass fat	M	9.9	N.S.	1.00	26.6	*	0.67	28.7	N.S.	1.57
	F	9.7		-	28.8		-	32.4		-
Muscle bone ratio	M	2.75	N.S.	0.111	5.02	N.S.	0.078	5.08	*	0.124
	F	2.57			5.07		-	5.64		-

+) Adjusted for conformation type and type of birth.

x) Including flank.

established. The proportion of shoulder was now 5% greater in males ($p < 0.001$), while that of the rib, prime loin and prime gigot was 3% ($p < 0.05$), 5% ($p < 0.001$) and 3% ($p < 0.01$) higher in the females, respectively. At the same time, the females were significantly fatter, or 8% ($p < 0.05$), the difference being relatively greater in subcutaneous than intermuscular fat. Muscle and bone, or the muscle: bone ratio, did not differ at this stage. Between 24 and 74 weeks, the proportion of shoulder remained unchanged in females while increasing in males, leading to a larger difference than before, or 11% ($p < 0.01$), which indicates a difference in relative growth rate over this time interval. This was met by proportionately heavier loin and gigot joints in females, the difference for the latter now being 7% ($p < 0.01$). While the effect on fatness was still similar, though non-significant due to the small number of animals, the males had now reached a 16% ($p < 0.05$) advantage in proportional bone weight, which, due to a smaller difference in muscle, gave the females an advantage of 0.56 units ($p < 0.05$) in muscle: bone ratio.

It is clear that, at constant age, the females were superior to males in the development of the later maturing tissues, and increasingly so with age. However, because of different shapes of the growth curve, the males at the earlier ages had reached a lower percentage of their mature weights than the females. Regressional analysis, over the first 24 weeks in life, revealed that tissue composition of the sexes was identical, when male carcasses weighed 10 - 12% more than female carcasses. As the difference in mature weight, between the two sexes, is likely to be of the order of 30 - 40%, it appears that at any equal stage of maturity the males would show a higher degree of development than females, which is in keeping with Hammond (1932). Our oldest group, however, does not support this conclusion, but, as previously discussed, the developmental potential between 24 and 74 weeks was probably penalized to a greater extent in the males by environmental limitations.

While sex effects on tissue composition can be described in terms of developmental order, this can not be adapted to describe differences in joint proportions. The noticeable difference in this respect, is the increasingly superior fore-quarter development in males, which, according to Bradfield (1968), is the direct effect of androgen stimulation of certain muscle groups in the neck region.

5.3 DISCUSSION

The present work has confirmed the order of development of the various carcass parts and tissues established by numerous earlier workers. One feature of the Edinburgh data, however, warrants closer consideration. While, before weaning, there was a gradual decline in the relative growth rate of bone, with increasing carcass weight, and a simultaneous increase in the relative growth rate of subcutaneous fat, this trend was reversed over the course of the feeding trial. Thus, the growth coefficient for bone was increased from 0.55 to 0.84, and that for SF reduced from 2.12 to 1.61, with muscle and IF maintaining constant relative rates. There may, however, be a dietary explanation to this phenomenon. It will be recalled that mid-way through the trial the diet had to be changed and the new diet was slightly poorer in ME value and richer in DCP, ash and calcium. Andrews and Ørskov (1970), Black (1974) and Ørskov, McDonald, Grubb and Pennie (1976) have all demonstrated significant effects of dietary protein concentration for lambs on the partition of energy between protein and fat reserves in the body. Thus, Ørskov *et al.* (1976) found a drastic increase in protein and water and a decrease in fat content of lambs, which were changed over from a low to a high protein diet at 28 kg live weight and killed at 40 kg. Although, in our case, the change in dietary protein concentration was by no means as drastic, it may well have been sufficient to affect muscle and fat proportions in the gain. Similarly, the increased calcium level could have affected bone growth and its composition, provided that this was a limiting factor before.

While only small genetic effects were detected on relative growth rates of tissues and joints, substantial differences between genotypes were observed in tissue composition and joint proportions, particularly in the Icelandic data. As these differences were related to developmental order, many critics would demand that the comparisons should be made at equal degrees of maturity, rather than at equal carcass weights. Obviously, the importance of this depends on, whether or how much the various genotypes differ in mature weight. Unfortunately, our data did not provide reliable information in this respect, but work continues in Iceland to establish body weight and composition at 'maturity'. It is unsafe to derive an estimate of relative genotype differences from the breeding flocks, particularly so for the

Edinburgh - cannon lines, due to the depressing hill environment, which might well disguise potential genetic differences in weight. Such information, however, suggests a difference of 5% in body weight between the L- and S-lines, in favour of the L-line, there being no difference in weight between the two Icelandic types. While our 'maturity' group in Edinburgh gave little valuable information on relative line differences in either weight or composition, because of lamb losses, the evidence from the Icelandic trial strongly suggests that the S-type.there would have a 20 - 25% lighter skeleton than the L-type at maturity. The same data indicates that the S-type might be approaching a lighter target muscle weight, of which we can not be sure, however, since muscle was still growing at considerable rate when the oldest sheep were killed.

While we accept the limitations of our data, in this respect, the evidence is strongly against the differences in carcass composition and proportions arising solely from unequal stages of maturity. Thus, it is clear, for the Icelandic sheep, that even when compared at equal level of fatness, both muscle: bone and fat: bone ratios were considerably higher in the S-type, despite 21% - 34% heavier carcass weight for the L-type. It can be shown, by regressional analysis, that for muscle: bone ratio to be the same in both types, the carcass would have to be 60 - 90% heavier in the L-type, depending on the stage of growth at which comparison was made. The corresponding difference in muscle + bone weight would be 55 - 85%, showing that carcass fat is not a confusing factor in this comparison. In Edinburgh, the differences were smaller and muscle: bone ratios were equal when L-carcasses were 20 - 50% heavier than those from the S-line. Nevertheless, such differences are unlikely to exist in potential mature weights between these lines.

As regards the ratio of SF to IF, some workers have suggested that this is unlikely to vary among genotypes, provided that percentage carcass fat is the same (Kempster, 1981 - personal communication). This view can not be fully substantiated as the Icelandic data showed an interaction between conformation type and the level of fatness. The indication was, that as the proportion of carcass fat increased, so would the difference in SF:IF ratio in favour of the S-type.

Looking at the proportions of carcass joints, it becomes immediately apparent, that the differences are larger than could conceivably

be explained by different mature size. Thus, for the prime loin to make up the same proportion of the carcass, the L-line in Edinburgh would be 50% heavier than the S-line, and even so, the proportions of shank and gigot would not be the same. The picture in Iceland is still more exaggerated. On this basis, we can confidently conclude that the selection procedures applied in each case have brought about changes, not only in carcass shape, but also in carcass proportions and composition, by means other than simply affecting mature weight. The major effects of selecting for a short cannon bone and blocky conformation have been to bring forward, and thus extend, the fattening phase, reduce the proportion of bone and to a lesser extent muscle in carcass growth, resulting in a higher muscle: bone ratio, and move weight from the extremities into the later developing regions of the trunk. The most obvious practical implications are, that the short-legged type of sheep will reach adequate level of 'finish' at an earlier age than a leggier animal and, provided that it is slaughtered within acceptable limits of fatness, will yield a marginally higher proportion of edible tissue in the carcass.

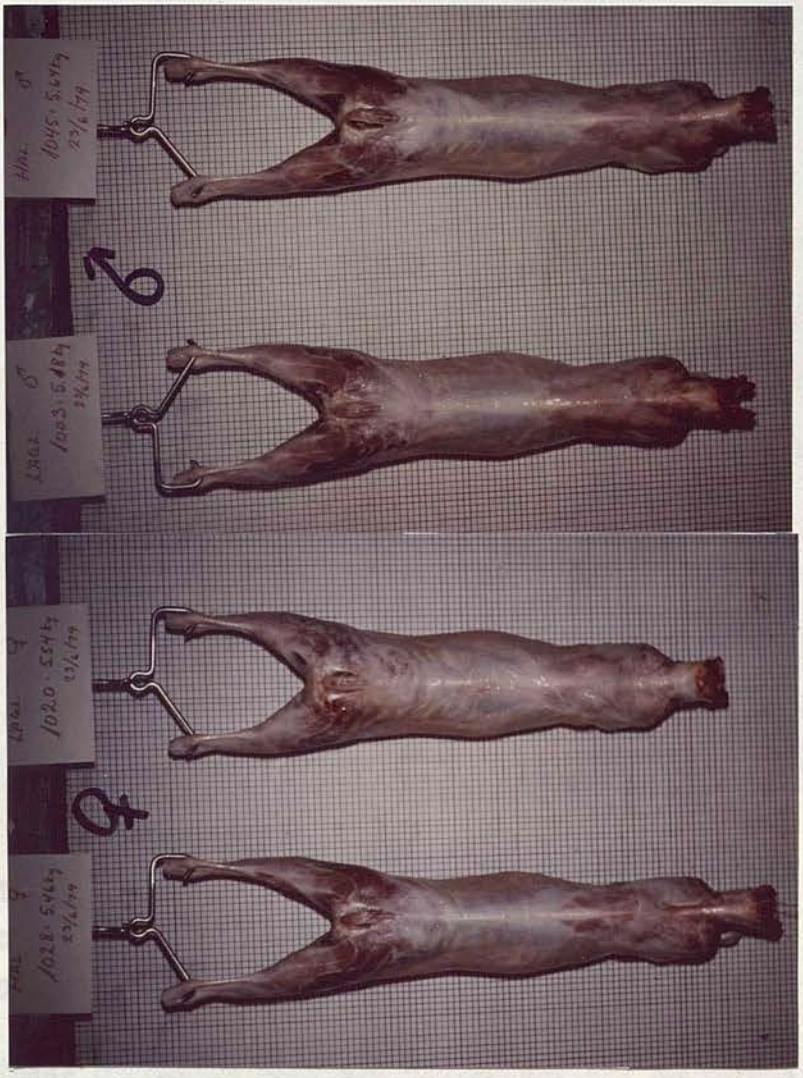
X

PLATE 5.1. DEVELOPMENTAL CHANGES IN CARCASS FORM AND COMPOSITION.

(ICELAND)

Pairs of S- and L-type carcasses (of similar weights), from 6 to 74 weeks of age. Apart from showing age related changes, these illustrate type differences and, to some extent, within type variation in carcass shape and composition.

S I X W E E K S O L D T W I N L A M B S.

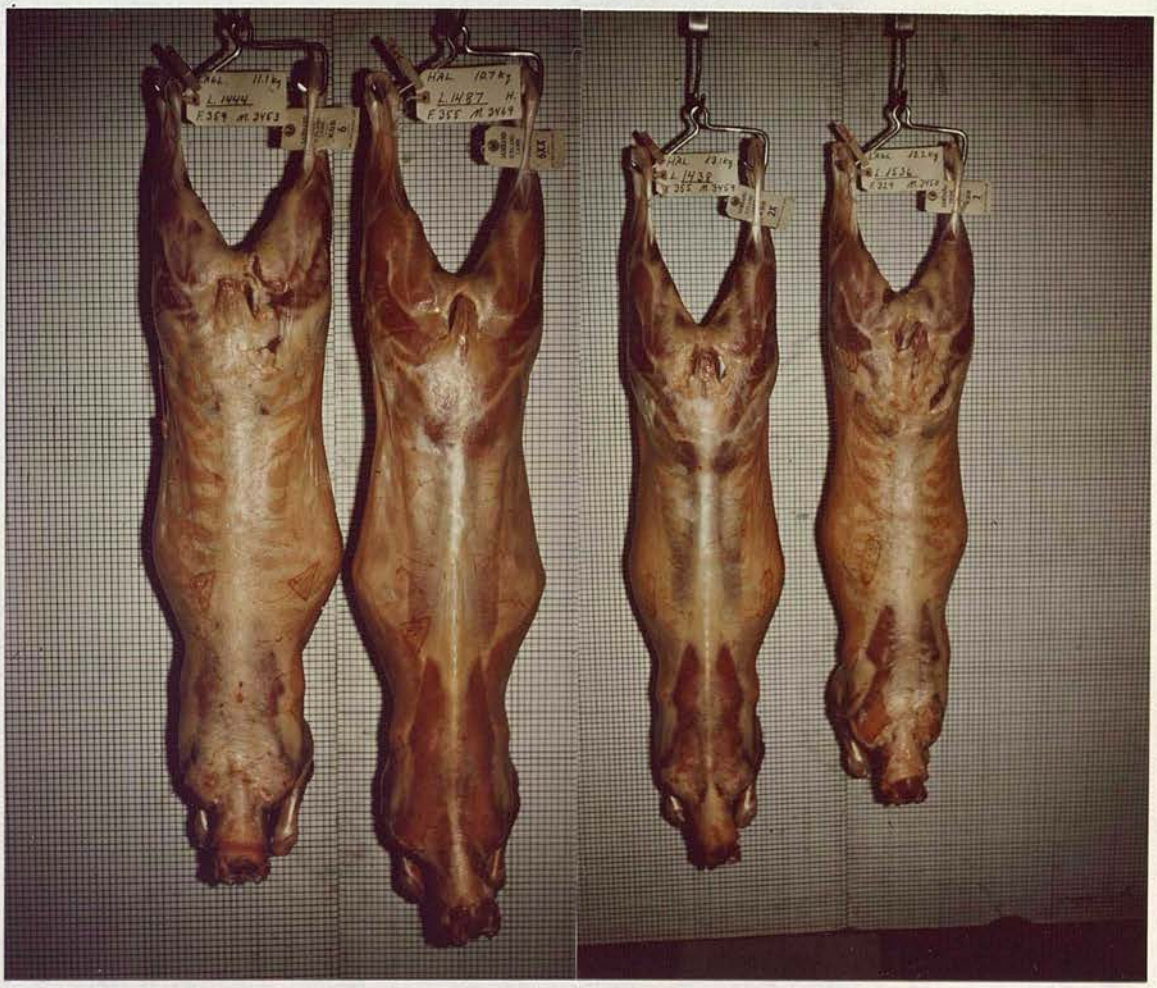


Type	LONG	SHORT	SHORT	LONG
Carcass wt. (kg)	5.5	5.5	5.2	5.6
Muscle %	69.6	64.3	69.5	69.4
Bone %	18.0	16.2	18.4	19.1
Fat %	12.3	19.5	12.2	11.4
Muscle:Bone Ratio	3.87	3.97	3.78	3.63

X) Carcass weight inclusive of kidney fat; tissue % refers to % of total dissected components (muscle+bone+fat), hence the values are higher than in the analyses based on pre-dissection carcass weight.

PLATE 5.1. (Continued).

16 WEEKS OLD LAMBS.



Type	SHORT	LONG	LONG	SHORT
Carc.wt.(kg)	11.1	10.7	13.1	13.2
Grade[x]	I	III	II	I*

These carcasses were not dissected, but commercially graded. Even at such light weights, the S-type carcasses were sufficiently well developed to fetch top grade, whereas the L-type carcasses were penalized. Note particularly the lack of subcutaneos fat and the poor development of the legs and loin of the latter.

x) Grade I is highest and III lowest - I* is a premium grade (good conformation and not over-fat).

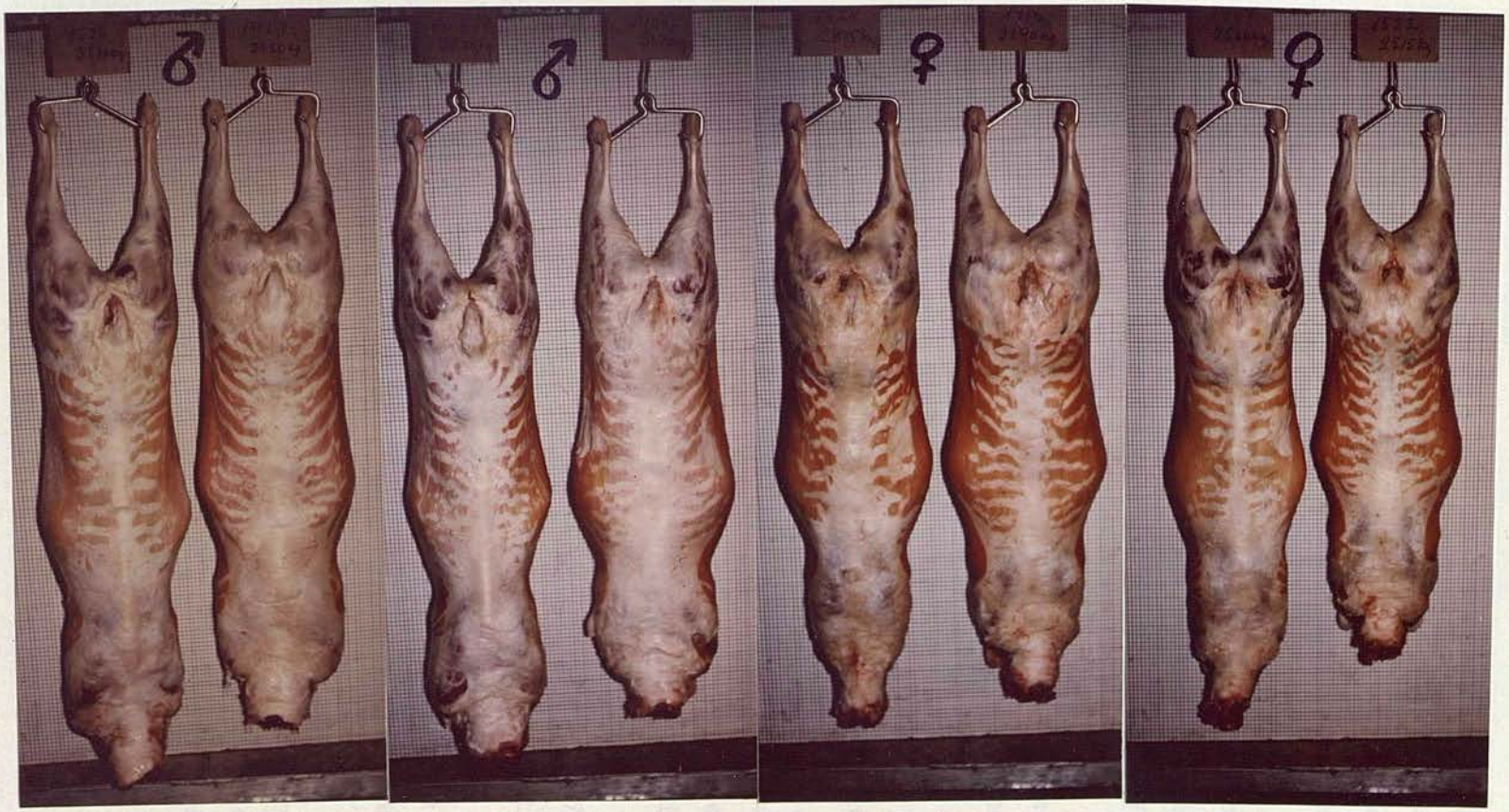
(Note different scale of pictures).

PLATE 5.1 (Continued). 20 – 24 WEEKS OLD LAMBS.

Type	LONG x	SHORT x	LONG	SHORT	LONG	SHORT
Carcass wt.(kg)	15.2	15.2	20.7	21.0	20.1	20.6
Muscle %	62.9	65.7	59.1	57.4	55.4	55.7
Bone %	13.9	11.3	13.0	10.7	12.5	9.7
Fat %	23.1	23.0	27.9	31.9	32.1	34.7
Muscle:Bone	4.51	5.81	4.55	5.36	4.43	5.75

x) Note different scale of picture.

PLATE 5.1. (Continued). 74 WEEKS GROUP.



Type	LONG	SHORT	LONG	SHORT	LONG	SHORT	LONG	SHORT
Carcass wt.	37.8	39.5	32.8	31.7	28.8	31.9	25.6	25.2
Muscle %	60.7	53.3	64.3	54.2	56.7	51.6	58.9	56.4
Bone %	12.9	10.0	13.2	10.1	10.0	8.7	11.6	9.3
Fat %	26.4	36.7	22.5	35.8	33.3	39.7	29.4	34.3
Muscle:Bone	4.70	5.34	4.88	5.37	5.69	5.91	5.06	6.04

CHAPTER 6.

DEVELOPMENT OF THE MUSCULATURE

6.1. INTRODUCTION

The Hammond school demonstrated that the growth gradients found within the whole carcass were also at work within each of the major carcass tissues. However, due to their coarse division of the carcass, these workers were unable to study, in detail, the developmental changes that take place within the musculature. The rapidly increasing knowledge in this field over the last two decades is largely to the credit of the individual muscle dissection technique evolved for cattle by Walker (1961) and adapted to sheep by Fourie (1962, 1965), and a similar technique developed by Butterfield (1963a) for cattle. Since this elaborate approach was first demonstrated, several comprehensive studies of muscle development have been conducted, including those of May (1964), Fourie (1965) (published by Jury, Fourie and Kirton, 1977), Lohse, Moss and Butterfield (1971), and Lohse (1973) in sheep, Butterfield (1963b), Butterfield and Berg (1966a, b), Charles and Johnson (1976) and Bergstrøm (1978) in cattle, and Richmond and Berg (1971[a]), Davies (1974b) and Coenaga and Carden (1979) in pigs. These workers have described the growth patterns of 70 - 90 individual carcass muscles and grouped them according to their anatomical location and/or their growth intensity in post-natal life.

The findings of Butterfield (1963b), using 57 cattle of heterogeneous nature, ranging in age from pre-birth (but near term) to 40 months, in general supported the Hammond school's centripetal theory of growth, while at the same time, identifying the abdominal muscles as those undergoing the greatest degree of development in post-natal life (see table 6.1.1.).

On the basis of these findings, Butterfield postulated that because of the natural developmental patterns, no commercial advantage was to be gained in muscle weight proportions, by seeking early maturity in livestock. While this conclusion has received considerable emphasis in subsequent literature, it must be remarked that the underlying experimental data was less than perfect. Thus, due to uneven distribution of animals from different genetic and environmental backgrounds, some confusion in the developmental order may have occurred.

Table 6.1.1. Relative growth of muscle groups from birth to four years.

(Relative to total muscle = 100)

Muscle group	
Distal intrinsic muscles of fore leg	60
Distal intrinsic muscles of hind leg	70
Proximal intrinsic muscles of fore leg	90
Muscles surrounding the spinal column	100
Muscles of the thorax and neck and those attaching fore leg to trunk	103
Proximal muscles of hind leg	104
Abdominal muscles	135

(from Butterfield, 1963b).

Butterfield (1963b) observed that not all individual muscles, or muscle groups, maintained constant growth ratios, relative to total muscle, from birth to maturity. Butterfield and Berg (1966a, b) examined the growth patterns over five age phases, using Huxley's growth coefficients. This led to the classification of growth patterns into six 'impetus' groups, three of which were mono-phasic (low, average or high) and three were diphasic (low-average, average-high or high-average), according to the magnitude of the growth coefficient, the 'average' not being significantly different from unity. A similar approach was adopted by Lohse et al. (1971) and Jury et al. (1977), and their classification of nine anatomically defined muscle groups (same as in present study) is summarized below, together with that of Butterfield and Berg (1966b).

Table 6.1.2. Classification of muscle groups according to growth impetus.

	Source of data		
	Butterfield & Berg (1966b)	Lohse et al. (1971)	Jury et al. (1977)
Muscle group	Cattle	Sheep	Sheep
1 - Proximal hind limb	H-A or L*	H	High-decreasing
2 - Distal hind limb	L	L	Low-decreasing
3 - Around spinal column	A	H-A	High-decreasing
4 - Abdominal	H-H or H	H	High
5 - Proximal fore limb	L-A	A-L	Low
6 - Distal fore limb	L-A or L	L	Low
7 - Joining neck to fore limb	H	A	Low-increasing
8 - Joining thorax to fore limb	A-H	A-L	Average
9 - Intrinsic of neck and thorax	L-A	L-A	Low-increasing

* H = High
A = Average
L = Low

There are several points regarding the information in table 6.1.2., which warrant closer consideration. (1) It is generally agreed that the greatest diversity in growth rates among individual muscles is observed soon after birth. Berg and Butterfield (1976) stated that, in general, the muscles tended to grow at similar average rates, once the birth weight of the total musculature had doubled. However, Lohse et al. (1971) and Jury et al. (1977) provided strong evidence for this not being so in sheep. (2) Contrary to Butterfield and Berg (1966a, b), both Lohse et al. and Jury et al. found the muscles around the spinal column (gr. 3), in particular m. longissimus dorsi, to grow at a high impetus rate in early life, while eventually decelerating to the average or lower than average rate. Similarly, Lohse et al. found the muscles of the proximal pelvic limb to continuously increase their proportion of total muscle, thus agreeing with Hammond (1932).

(3) It is evident, that within each anatomical group, the constituent muscles exhibit a marked diversity in their relative growth rates. A similar diversity would also be observed within such functional units as were suggested by Fowler (1968) and Fowler and Livingstone (1972). (4) While acknowledging the general principle of centripetal growth patterns, these two studies on sheep, are not in complete agreement, and both differ markedly from the cattle study. This discrepancy may rise from a combination of several factors. (a) There may be a true species difference between cattle and sheep, though unlikely. (b) The two sheep studies were undertaken with different breeds, and (c) the sexes were also different. (d) Despite the belief of many workers (Berg and Butterfield, 1976) that muscle development is virtually independent from nutritional history, the evidence is inconclusive, and the possibility of differential nutritional effects can not be excluded. (e) The somewhat arbitrary partition into growth phases may not always result in the truest classification, as whether a particular muscle is mono-di- or indeed multiphasic in its growth patterns. In fact, the changes observed in impetus patterns are most likely continuous rather than discrete in nature.

Breed effects on muscle development have been studied by comparing relative growth rates and/or the proportions of individual muscles, muscle groups or total contents of muscle in carcass joints, in relation to total muscle. In brief, two schools of thought have arisen with respect to the influence of breed, in particular, conformation, on muscle weight distribution. The first school maintains, that muscle weight distribution is a relatively constant and unchangeable characteristic, and that such variation as may exist is too small to be of economic significance. Thus, Butterfield (1963b) stated: 'Much money and time is undoubtedly wasted by breeders in efforts to improve the distribution of muscle weight on the carcasses of beef animals', and the same view was emphasized by Berg and Butterfield (1976). Similarly, Jury et al. (1977), while showing significant breed effects on the growth coefficients for 13 individual muscles and four out of the nine muscle groups, concluded that 'the supposedly superior blocky conformation of the Southdown x Romney has conveyed no superiority in terms of distribution of the more valuable muscles relative to the leggier Romney'. There are, however, several interesting features in the original data of Fourie (1965) which are

not elucidated in the re-analysis by Jury et al (1977). Thus, for instance, the pure Southdown had a consistently higher proportion (7% at 16 and 25 weeks of age) of the longissimus dorsi muscle, compared with the pure Romney.

The second school of thought, while accepting a high degree of resistance to genetic modification, claims that both individual and interbreed variations in muscle distribution, of substantial magnitude, have been demonstrated. It is argued that such variation could be successfully exploited by genetic selection, if a suitable technique for assessment could be found (Seebeck, 1973b), Martin, Walters and Whiteman (1966) found steer carcasses of 'choice' conformation to have a significant advantage in the percentage of thick, high-value muscles, and breed differences between Brahman cross and Africander cross cattle were reported by Seebeck (1973b). In pigs Richmond and Berg (1971a) found a difference between the Duroc Yorkshire and the Yorkshire breeds in the proportion of muscles surrounding the spinal column. Davies (1974b) also found the Pietrain to be superior, to the Large White, with respect to the development of femoral muscles and the longissimus dorsi, while the brachial muscles grew relatively faster in the Large White pigs. Similarly, after a comparison of Landrace, Hampshire and Duroc Jersey pigs, Goenaga and Carden (1979) strongly rejected the view that muscle weight distribution in pigs showed little or no variation.

As far as sheep are concerned, there have been few studies of breed effects on muscle distribution, involving total individual muscle dissection, other than that of Fourie (1965). Seebeck (1968a) found pure bred Merinos to contain 16% more muscle in the neck and 6% less in the thorax than the Dorset Horn x (Merino x Border Leicester) at equal total muscle weight. Furthermore, Taylor, Mason and McLelland (1980) compared lambs of four breeds (Soay, Southdown, Finnish Landrace and Oxford Down) at equal stages of maturity and demonstrated the superiority of the Southdown over the other breeds in the combined proportion of 12 individual muscles, these comprising 43.4% of total muscle in the Southdown, compared with 39.8% in the Oxford Down. The most marked difference was found in the longissimus dorsi muscle, or 20% in favour of the Southdown relative to the Finnish Landrace. The authors concluded that 'significant breed differences of noticeable magnitude

can be found, and not only because extremes such as feral and down breeds are being compared'.

In conclusion, it would appear unquestionable that variation exists in muscle weight distribution which at least, is of biological interest, while the commercial value of this may be circumstantial and continues to be debated.

Sex is a recognized factor in influencing the muscle weight distribution in domestic animals. In their review of cattle growth and development, Berg and Butterfield (1976) stated that: 'the difference in rate of growth of individual muscles in bulls, steers and cows can be considered on the basis of the bull being the only 'sex' which fully utilizes the inate potential to grow differentially'. This would equally apply for sheep.

Lohse (1973) studied the muscle weight distribution of ewes and rams from birth to 730 days of age, ranging in live weight from 3 to 40 kg. Twenty five muscles and three muscle groups were classified differently in the two sexes. The greatest differences were observed in the neck region, the combined group of intrinsic neck and thorax muscles growing significantly faster in the rams with increasing age. The muscles in the proximal hind limb were found to reach an average growth plateau earlier in ewes than in rams, indicating earlier maturity of these muscles in the female sex. The opposite effect was observed by Jury et al. (1977), i.e. the relative growth rate of the 'pelvic' muscles declined more rapidly with age in rams than in ewes. Other than that, the two studies appear to be in general agreement, and both highlight the superior fore-quarter development in the male. As referred to earlier, the enhanced growth of some neck muscles in the male is thought to be the direct response to androgen stimulation (Bradfield, 1968). In general, the two sexes have been found to have similar muscle proportions at birth, but to diverge before the attainment of puberty. Relating to the commercial aspect, Lohse (1973) concluded that only in 'older' rams, might the heavy neck muscles have an adverse effect on muscle weight distribution.

6.2. RESULTS

a) Common developmental patterns.

In Edinburgh, the patterns of muscle development were studied in terms of total muscle in joints (table 6.2.3.) and 14 individual muscles

(Appendix 10), while in Iceland both relative weight increases, over defined age intervals and relative growth coefficients are presented for nine anatomically defined muscle groups (figure 6.2.1. and table 6.2.1.) and for the 69 individually dissected muscles or combined muscles (Appendeces 10 and 11). The twofold presentation serves to illustrate, how the two methods are synonomous in revealing the same patterns.

The following discussion of common developmental order is mainly based on the Icelandic material, which was more comprehensive in this respect. A classification of muscles and muscle groups, according to growth intensity, similar, though not identical, to that of previous workers (e.g. Berg and Butterfield, 1976), is illustrated below:

Very high:		$b > 1.20$
High	:	$1.20 \geq b \geq 1.05$
Average	:	$1.05 > b > 0.95$
Low	:	$0.95 \geq b \geq 0.80$
Very low	:	$b < 0.80$

This classification is somewhat arbitrary, and the growth coefficients have not been tested against the dividing points, however, the significance levels can be determined from the standard errors.

The growth coefficients were estimated for various age intervals and when found to differ significantly from one period to another, the respective muscles were classified as di- or tri-phasic (any combination of VH, H, A, L and VL). The majority of muscles showed uniform growth patterns within age intervals 0 - 16 weeks and 16 - 74 weeks, (i.e. quadratic trends were non-significant); consequently, the growth coefficients over these two phases are presented for all the muscles (Appendix table 11.2.a.), while details of those muscles behaving differently are shown in Appendix table 11.2.b. It is acknowledged that the classification adopted can be no more than a simplification of the reality and could be subject to modification by more frequent or different slaughter ages.

It is immediately apparent (figure 6.2.1. and table 6.2.1.) that the different muscle groups grew at vastly different rates, relative to total muscle. Each group will now be considered separately with some reference to individual constituent muscles.

Figure 6:2:1. RELATIVE GROWTH OF MUSCLE GROUPS — ICELAND

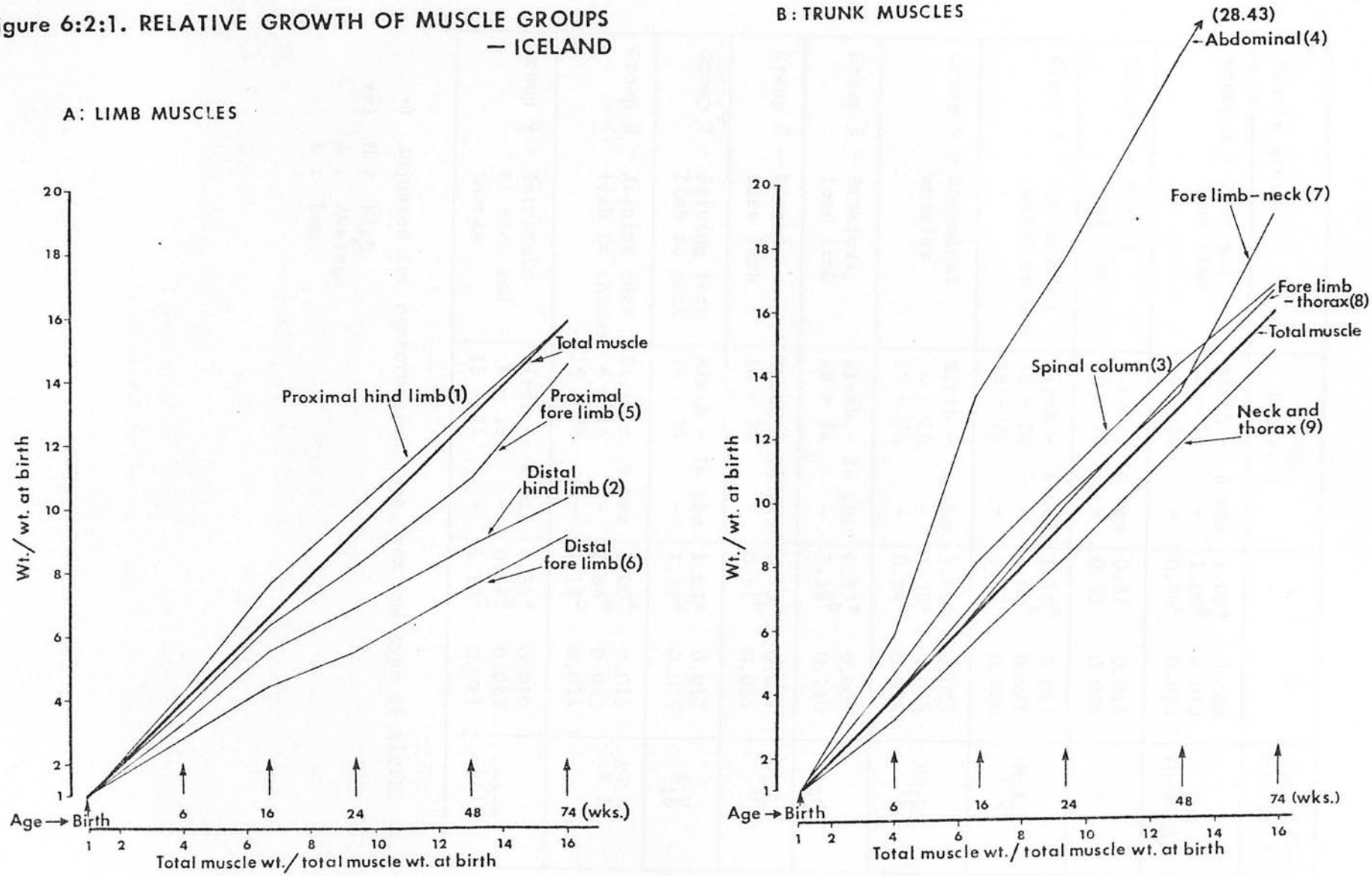


Table 6.2.1. Relative growth coefficients, relating muscle groups to total muscle weight[+]. (Iceland).

Muscle group	Age interval	b	SE	Classification[++]
Group 1 - Proximal hind limb	Birth - 6 wks	1.05[a]	0.008	H-A (H-A-LA)
	6 - 16 -	1.00[b]	0.018	
	16 - 74 -	0.96[c]	0.014	
Group 2 - Distal hind limb	Birth - 16 wks	0.87	0.014	L
	16 - 74 -	0.83	0.025	
Group 3 - Surrounding spinal column	Birth - 6 wks	1.10[a]	0.011	H-A-L
	6 - 24 -	1.00[b]	0.021	
	48 - 74 -	0.83[c]	0.070	
Group 4 - Abdominal muscles	Birth - 6 wks	1.29[a]	0.025	VH-L
	6 - 16 -	1.38[a]	0.066	
	16 - 74 -	0.94[b]	0.024	
Group 5 - Proximal fore limb	Birth - 24 wks	0.93[a]	0.008	L-H
	48 - 74 -	1.18[b]	0.110	
Group 6 - Distal fore limb	Birth - 16 wks	0.75[a]	0.011	VL-L
	16 - 74 -	0.91[b]	0.021	
Group 7 - Joining fore limb to neck	Birth - 16 wks	1.01[a]	0.017	A-H
	16 - 74 -	1.19[b]	0.024	
Group 8 - Joining fore limb to thorax	Birth - 6 wks	1.00[a]	0.015	A-L-H
	6 - 16 -	0.88[b]	0.042	
	16 - 74 -	1.12[c]	0.024	
Group 9 - Intrinsic of neck and thorax	Birth - 6 wks	0.84[a]	0.010	L-A-H
	6 - 16 -	0.97[b]	0.023	
	16 - 74 -	1.10[c]	0.023	

+) Adjusted for conformation type, sex and type of birth.

++) H : High
A : Average
L : Low

Group 1 (Muscles of the proximal hind leg) has been classified as di-phasic, high$_{6}^{-}$average. However, the significant change in growth coefficients at 16 weeks, though small, would justify a further partitioning (H$_{6}^{-}$A$_{16}^{-}$L). At birth, this group constituted 26.9% of the whole, this had increased to 28.7% ($p < 0.001$) by six weeks, remained constant for the subsequent ten weeks, but had fallen again to the initial value of 26.9% at 74 weeks of age. Within the group, the individual muscles showed diverse impetus growth patterns, ranging from high to very low, and five were defined as di-phasic (H-A, H-L, or A-L). The muscles gluteus medius, semimembranosus and semitendinosus grew fastest and increased their weights approximately 18-fold over the course of 74 weeks. The smaller, deeper muscles grew more slowly, the muscle gemellus only increasing its birth weight 9 times over the same period.

Group 2 (Muscles of the distal hind limb) grew constantly slower than the rest of the musculature and was classified as mono-phasic, low impetus group. This group comprised 7.0% of total muscle at birth, which fell gradually to 4.5% at 74 weeks ($p < 0.001$). The decline in proportion was somewhat steeper over the first six weeks than subsequently. All but two of the constituent muscles were mono-phasic (L or VL). The gastrocnemius showed a fall in relative growth rate at 16 weeks (L-VL), while the reverse was observed for the peroneus tertius (+ long extensor group) (VL-A).

Group 3 (Muscles surrounding the spinal column) showed a tri-phasic growth pattern, high-average-low. At birth it was 13.4% of total muscle, reached a maximum of 15.5% at six weeks ($p < 0.001$), but had declined to 14.1% at 74 weeks ($p < 0.001$). There was only a marginal change in the proportion of this group over the commercial range in slaughter age (15.2% - 15.1%). The largest muscle in the group, the longissimus dorsi, showed the greatest relative weight increase, or 18.3-fold over the 74 weeks. Its initial growth coefficient was 1.19, which subsequently declined to 1.04 ($p < 0.01$) and 0.83 ($p < 0.05$) over age intervals 6 - 24 weeks and 48 - 74 weeks, respectively. The psoas major showed a similar pattern, while the other four were classified as either A or L impetus muscles.

Growth gradients were tested for within the longissimus dorsi muscle, by comparing weight changes in its different parts. Only in Edinburgh, were separate growth coefficients calculated, while in Iceland

the proportional changes in the thoracic, lumbar and sacral portions were examined (table 6.2.2.).

Table 6.2.2. Developmental changes within the muscle *Longissimus dorsi*.

A: Relative growth coefficients, relating different parts of the muscle to total muscle weight. (Edinburgh).

Part of *L. dorsi*	Pre-trial (12 - 19 wks) b	SE	On trial (19 - 48 wks) b	SE
In shoulder	0.66^{a}	0.087	0.94	0.094
In rib	0.97^{b}	0.067	0.97	0.145
In loin	1.22^{c}	0.082	1.16	0.060

B: Changes in proportions of the different parts. (Iceland)

Age	Percentage of total *L. dorsi* Thoracic part	Lumbar part	Sacral part
Birth	$42.5^{a} \pm 0.73$	$48.6^{a} \pm 0.90$	$8.9^{a} \pm 0.53$
6 weeks	$42.0^{a} \pm 0.89$	$51.4^{b} \pm 0.86$	$6.7^{b} \pm 0.36$
20-24 -	$38.6^{b} \pm 0.41$	$55.1^{c} \pm 0.38$	$6.4^{b} \pm 0.26$
74 -	$39.4^{b} \pm 0.73$	53.0^{b} 0.39	7.6 $\pm$ 0.48

A striking differential growth pattern was revealed, there being a gradient of increasing growth intensity towards the lumbar section. Thus, the percentage of the lumbar part increased by 6.5 units ($p < 0.001$) from birth to 20 - 24 weeks, while that of the thoracic and sacral portions was reduced by 3.9 and 2.5 units ($p < 0.001$), respectively. The later reverse tendency, shown in the table, only appeared after 48 weeks of age.

Group 4 (Abdominal muscles) showed the greatest relative weight increase of all the muscle groups, or 28.4-fold over the range studied. However, it was only for the first 16 weeks that this group grew faster than the total muscle, and it was classified as di-phasic, very high-low

impetus group. The data suggests a peak rate of relative growth between six and 16 weeks. Proportionate to total muscle, group 4 weighed 5.7% at birth, reached a maximum of 10.9% at 16 weeks ($p < 0.001$) and comprised 10.5% of the whole at 74 weeks. The four major abdominal muscles were either VH-A or VH-L. Among them, there was an inwards gradient of increasing growth intensity in the first age phase, the growth coefficients being 1.24, 1.26, 1.39 and 1.50 for the muscles obliq. abdom. externus, rectus abdom., transversus abdom. and obliq. abdom. internus, respectively.

Group 5 (Muscles of the proximal fore limb) has been classified as di-phasic, low-high impetus group. Over the range studied, this group increased its weight relatively less than the total muscle, or 14.6-fold. It constituted 14.2% of total muscle at birth, reached a minimum of 12.0% at 24 weeks ($p < 0.001$) and had risen again to 12.9% at 74 weeks ($p < 0.001$). All the constituent muscles showed a tendency for a di-phasic pattern similar to that of the group, the largest muscles, infraspinatus, supraspinatus and triceps brachii dominating in deciding the change-over point.

Group 6 (Muscles of the distal fore limb) grew continuously at a lower rate than total muscle and made the smallest relative weight gain, post-natally, of all the groups, or 9.2-fold. However, the pattern changed at 16 weeks and the group was classified as di-phasic, very low-low impetus group. Its proportion of the whole was 5.2% at birth and 3.0% at 74 weeks ($p < 0.001$).

Group 7 (Muscles joining the fore limb to the neck) grew at an average rate to 16 weeks and significantly faster thereafter ($A\text{-}_{16}H$). Its proportion of the whole was only marginally (non-significantly) reduced from 7.6% at birth to 7.3% at 16 weeks, while having been increased to 9.0% ($p < 0.001$) at 74 weeks. One muscle, the serratus ventralis, showed a tri-phasic (H-A-H) growth pattern, while the other three were di-phasic (L-H or VL-VH). It should be noted that, in strict terms, the thoracic part of the serratus ventralis belongs to group 8, however, the whole muscle was included in group 7, in accordance with Lohse et al. (1971) and Jury et al. (1977).

Group 8 (Muscles joining the fore limb to the thorax) differed from all the other groups by exhibiting a declining-increasing, tri-phasic ($A\text{-}_{6}L\text{-}_{16}H$) growth pattern. It comprised 6.8% of total muscle at birth, 6.3% at 16 weeks ($p < 0.01$) and 7.0% at 74 weeks ($p < 0.01$). The

Table 6.2.3. Relative growth coefficients, relating muscle weight in joints to that of total carcass muscle.

A: Edinburgh - 98 lambs on trial (adjusted to constant daily D.M. intake).

Muscle in:	Overall b	Overall SE	b at total carc. muscle wt:+ 5.0 kg	7.5 kg	10.0kg
Shoulder + breast	1.01	0.021	0.92	1.01	1.07
Neck	0.90	0.109			
Shank	0.64	0.078	0.94	0.63	0.41
Total rib	1.18	0.043			
Prime loin	1.13	0.050	1.31	1.12	0.99
Loin flank	0.95	0.179	1.72	0.94	0.38
Total gigot	0.94	0.020			

B: Iceland - 56 lambs from 6 - 24 weeks.

Muscle in:	Overall b	Overall SE	b at total carc. muscle wt:+ 5.0 kg	7.5 kg	10.0 kg
Prime shoulder	1.00	0.015			
Secondary shoulder[x]	0.96	0.017	0.92	1.02	1.09
Prime rib	0.94	0.026	0.85	1.02	1.14
Secondary rib	1.11	0.031	1.20	0.99	0.84
Prime loin	1.05	0.025			
Loin flank	1.34	0.063	1.50	1.12	0.85
Prime gigot	0.97	0.014			
Gigot flank	1.12	0.068			

+) Calculated for those joints showing significant quadratic trends.

x) Breast + shank + neck.

tri-phasic nature was only significant for the pectorales muscles, the other two being di-phasic (A-H).

Group 9 (Intrinsic muscles of the neck and thorax). This group consists of 15 muscles (or groups) of most diverse growth patterns, while being as a unit classified as a tri-phasic, low$_{6}$-average-$_{16}$high impetus group. It will be shown later (Ch. 6.2.b.) that much of this diversity was related to sex. Overall, the group comprised 13.5% of total muscle at birth, 10.6% at 16 weeks ($p < 0.001$) and 12.3% at 74 weeks ($p < 0.001$). While gaining relatively less weight than the average over the whole range studied, this group, together with group 7, showed the highest relative weight gains of all between 24 and 74 weeks. The individual muscles were classified as either mono-phasic (L) or di- or tri-phasic (A, L, VL-increasing).

The carcass joints can not be equated with the anatomical muscle groups, in developmental terms; these are, however, commercially of even greater interest. As far as the jointing was comparable, the relative growth rates (table 6.2.3.) were similar for both the experiments. The rib and loin joints showed a proportional weight increase as development progressed. The loin flank showed the highest relative rate of all the cuts initially, while declining in rate, with increasing muscle weight, below the average. The whole shoulder was close to the average impetus, and the shank and gigot grew at significantly lower rates than the rest of the musculature.

b) Genotype effects on the development and distribution of muscles.

In Edinburgh, no significant effects of genotype were observed on the relative growth rates of total muscle in joints, or of those individual muscles studied. Such effects were demonstrated in Iceland for one muscle group and 13 individual muscles, although generally small (table 6.2.4.). Three muscles of the proximal fore limb grew faster in the L-type for the first 16 weeks and so did the group as a whole. Five muscles in the thorax-neck region also showed higher relative rates in the L-type, as well as the muscles semitendinosus and transversus abdominis. In contrast, the S-type had higher growth coefficients for the muscles pectineus, psoas major and rectus abdominis. Thus, with respect to relative growth patterns, the effects of conformation type were mainly confined to the fore-quarter, within which eight muscles grew relatively faster in the L-type at some stage of growth.

Table 6.2.4. Effect of conformation type on relative growth rates of muscles.+ (Iceland).

Muscle/group	Conf. type	Age:0-16 wks. b	SE	Signific. of diff.	Age:16-74 wks. b	SE	Signific. of diff.
Muscle group 5	L	0.96	0.011	**	0.98	0.024	N.S.
	S	0.91	0.012		1.03	0.024	
Semitendinosus (1)	L	1.07	0.018	*	1.04	0.041	N.S.
	S	1.01	0.018		1.07	0.039	
Pectineus (1)	L	1.02	0.028	*	0.81	0.048	N.S.
	S	1.10	0.028		0.93	0.047	
Psoas major (3)	L	1.06	0.022	*	0.91	0.040	N.S.
	S	1.13	0.022		0.93	0.041	
Rectus abdominis (4)	L	1.20	0.028	**	0.90	0.048	N.S.
	S	1.33	0.028		0.97	0.047	
Transv. abdominis (4)	L	1.43	0.038	*	0.81	0.055	N.S.
	S	1.30	0.038		0.87	0.054	
Supraspinatus (5)	L	1.00	0.016	***	0.91	0.042	N.S.
	S	0.91	0.016		0.99	0.041	
Teres major (5)	L	1.01	0.023	*	0.93	0.079	**
	S	0.93	0.023		1.22	0.076	
Triceps brachii (5)	L	0.95	0.011	***	0.94	0.026	N.S.
	S	0.89	0.012		0.95	0.026	
Brachiocephalicus (7)	L	0.94	0.032	**	1.19	0.057	N.S.
	S	0.80	0.032		1.08	0.056	
Latissimus dorsi (8)	L	0.99	0.020	*	1.09	0.046	N.S.
	S	0.93	0.020		1.14	0.045	
Rhomboideus (8)	L	1.04	0.036	*	1.24	0.065	N.S.
	S	0.94	0.036		1.09	0.063	
Complexus (9)	L	0.81	0.025	N.S.	1.25	0.053	*
	S	0.76	0.026		1.09	0.051	
Longissimus costarum (9)	L	0.94	0.044	N.S.	1.25	0.081	**
	S	0.98	0.045		0.92	0.078	

+) Adjusted for sex and type of birth.

(Type differences in other muscles or muscle groups were non-significant)

Significant genotype differences were observed in both experiments, with respect to muscle weight distribution at constant total muscle weight. In Edinburgh (table 6.2.5.), the main effects were on the loin and gigot joints. The L-line had 5% more muscle in the gigot ($p < 0.001$) and 8% less in the prime loin ($p < 0.01$) than the S-line, the C-lambs being intermediate. A less regular effect was found on the loin flank, whose muscle was though heaviest in the S-line, or 18-25% ($p < 0.01$). Muscle in the shank was 12% heavier in the L-line than in the S-lambs ($p < 0.05$), while all three lines were similar regarding the shoulder and breast.

Contrary to the Edinburgh results, the two types in Iceland (table 6.2.6.) were identical in the proportions of group 1 and group 2 muscles, and consequently in total prime gigot muscle. The L-type had superior development of all the fore-quarter groups except group 8 (fore limb to thorax), the differences ranging from 3% to 6% ($p < 0.05 - 0.001$). In contrast, the muscles surrounding the spinal column and the abdominal muscles were 4-6% and 8-10% heavier in the S-type ($p < 0.05 - 0.001$), respectively. These differences were reflected in the proportions of muscle weight in the various joints. Thus, the L-lambs had a 6% advantage ($p < 0.001$) over S-lambs in shoulder muscle (prime and secondary equal), met by differences of 14% and 29% ($p < 0.001$) in the prime loin and loin flank, respectively, in favour of the S-lambs.

Looking at individual muscles, (Appendix 12), the L-type was most superior in the fore-quarter muscles supraspinatus (16%), brachialis (16-18%) fore-flexor group (5-15%), brachiocephalicus (8-9%) and obliqus capitis posterior (13-22%), while also having heavier semitendinosus (8-12%) and eight small muscles in the hind leg. Conversely, the S-type had the greatest advantage in the abdominal muscles (6-16%) and in the longissimus dorsi (8-11%). An interesting difference was also observed in weight proportions within the l. dorsi muscle. At 20 - 24 weeks the lumbar portion was 56.5% of the whole in the S-type, compared with 53.4% in the L-type ($p < 0.001$). The same effects were observed in Edinburgh, and also in the weight relation of the whole l. dorsi with total muscle. The only other outstanding effects were found on the gigot muscles quadriceps femoris, gastrocnemius and extensor digitorum longus, all of which were positively related to cannon bone length in the Edinburgh sheep.

Table 6.2.5. Effect of cannon line on muscle weight distribution+. (Edinburgh).

Muscle in:	Line	Wt. (g) Mean	SE	% of carcass muscle	Relative diff. (C=100)	Significance level L-C	L-S	C-S
Shoulder + breast	L	2632	17.0	32.9	100	N.S.	N.S.	N.S.
	C	2624	15.2	32.8				
	S	2658	19.6	33.2	101			
Neck	L	220	7.2	2.8	94	N.S.	*	N.S.
	C	233	6.8	2.9				
	S	245	9.4	3.1	105			
Shank	L	174	4.2	2.2	108	*	**	N.S.
	C	161	3.4	2.0				
	S	155	4.4	1.9	96			
Rib	L	876	10.0	11.0	101	N.S.	N.S.	N.S.
	C	870	10.0	10.9				
	S	898	13.6	11.2	103			
Prime loin	L	862	13.2	10.8	93	**	**	N.S.
	C	922	12.6	11.5				
	S	940	16.4	11.8	102			
Loin flank	L	137	7.4	1.7	107	N.S.	**	**
	C	128	6.2	1.6				
	S	160	9.8	2.0	125			
Gigot	L	3082	17.8	38.5	101	N.S.	***	***
	C	3050	16.2	38.1				
	S	2930	20.2	36.6	96			

+) Estimated by regressions at 8.0 kg carcass muscle weight and adjusted to constant daily D.M. intake.

Table 6.2.6. Effect of conformation type on muscle weight distribution[+]. (Iceland).

A: Anatomical muscle groups.

Muscle group	Conf. type	Carcass muscle = 5.0 kg			Carcass muscle = 10.0 kg		
		Wt. as % of Carc. muscle	Relative diff. (S = 100)	Significic. of diff.	Wt. as % of carc. muscle	Relative diff. (S = 100)	Significic. of diff.
Gr.1 - proxim. hind limb	L S	28.6 28.4	100	N.S.	27.8 27.8	100	N.S.
Gr. 2 - Distal hind limb	L S	5.5 5.6	99	N.S.	4.9 4.9	100	N.S.
Gr. 3 - Around spinal column	L S	14.7 15.6	94	***	15.0 15.7	96	*
Gr. 4 - Abdominal muscles	L S	9.2 10.0	92	*	10.2 11.4	90	***
Gr. 5 - Proxim. fore limb	L S	13.1 12.3	106	***	12.3 11.6	106	***
Gr. 6 - Distal fore limb	L S	3.5 3.4	103	N.S.	3.1 2.9	104	***
Gr. 7 - Fore limb to neck	L S	7.6 7.2	106	**	8.1 7.7	105	***
Gr. 8 - Fore limb to thorax	L S	6.5 6.5	100	N.S.	6.7 6.7	99	N.S.
Gr. 8 - Neck and thorax	L S	11.0 10.6	103	*	11.8 11.1	106	***

For absolute weights and standard erros - see Appendix 12.

Table 6.2.6. (continued).

B: Commercial joints (total muscle = 10.0 kg)

Muscle in:	Type	Wt. (g) Mean	SE	% of carcass muscle	Relative diff. (S=100)	Signific. level
Prime shoulder	L	2104	19.6	21.0	106	***
	S	1993	20.2	19.9		
Secondary shoulder[x]	L	1768	22.2	17.7	106	***
	S	1673	24.6	16.7		
Prime rib	L	644	12.2	6.4	101	N.S.
	S	639	14.2	6.4		
Secondary rib	L	617	13.4	6.2	97	N.S.
	S	637	16.2	6.4		
Prime loin	L	818	12.6	8.2	88	***
	S	933	15.6	9.3		
Loin flank	L	306	14.4	3.1	77	***
	S	398	22.0	4.0		
Prime gigot	L	3530	31.0	35.3	100	N.S.
	S	3518	33.8	35.2		
Gigot flank	L	207	8.8	2.1	100	N.S.
	S	206	9.6	2.0		

+) Estimated by regressions and adjusted for sex and type of birth.

x) Muscles in neck + below deflanking line.

c) Effects of sex on the development and distribution of muscles.

Three muscle groups and 18 individual muscles exhibited significantly different growth patterns in the two sexes at some stage of development (table 6.2.7.) The most substantial difference was found in muscle group 9 (intrinsic of neck and thorax), which grew faster in males over the whole range studied, and increasingly so after 16 weeks of age. This was mainly due to five individual muscles, of which the splenius cervicalis showed the highest degree of masculine effects. Muscle group 8 (fore limb to thorax) grew relatively faster in the females, which could be contributed to the pectorales and latissimus dorsi muscles, and the same tendency was observed for group 1 (proximal hind limb), though not significant. Group 3 (surrounding the spinal column) showed no sex effect during the earlier stages of development, but grew at a significantly lower rate in the females after 48 weeks of age. While significant sex effects were found on eight muscles in other locations, these were not sufficient to alter the patterns of the respective muscle groups.

With regard to muscle weight distribution at equal ages (table 6.2.8.), the largest differences were found in groups 1, 7 and 9, the effects on groups 2 and 8 also approaching significance. The females were born with a higher percentage of group 1 muscles ($p < 0.05$); that advantage was increased with age and amounted to 2.9 percentage units, or 11% ($p < 0.001$) at 74 weeks. A similar, but smaller difference was found in group 2 muscles (distal hind limb), though only significant ($p < 0.01$) at 20-24 weeks. The muscles in group 8 were proportionately heavier in the males at birth (11% - $p < 0.05$); however, that difference was reversed with age. As expected the males expressed the greatest superiority in the development of muscle groups 7 and 9, especially in the latter. While both sexes were identical at birth, regarding the percentage of group 9 muscles, the different growth patterns resulted in a steeper initial fall in proportion of that group in the females, reaching a plateau of approximately 10.5%, whereas, in the males, the proportion of muscles in group 9 reached a minimum of 12.3% at 20-24 weeks, and had been increased to 14.0% by 74 weeks, or 33% higher than in the females ($p < 0.001$).

Considering individual muscles, it is apparent that the greatest male effects were exerted on the muscles splenius and longissimus

Table 6.2.7. Effect of sex on relative growth rates of muscles.[+] (Iceland).

A: Birth - 16 wks. and 16 - 74 wks.

Muscle/group	Sex	Age: 0-16 wks. b	SE	Signific. of diff.	Age: 16-74 wks. b	SE	Signific. of diff.
Muscle group 8	M	0.94	0.018	*	1.09	0.027	N.S.
	F	1.00	0.017		1.16	0.039	
Muscle group 9	M	0.90	0.013	**	1.16	0.026	**
	F	0.85	0.012		1.03	0.038	
Gluteus medius (1)	M	1.09	0.027	N.S.	0.99	0.037	*
	F	1.06	0.026		1.15	0.055	
Semimembranosus (1)	M	1.12	0.027	N.S.	0.91	0.029	*
	F	1.07	0.026		1.02	0.043	
Oburators (1)	M	1.00	0.041	N.S.	1.10	0.059	*
	F	1.04	0.039		0.85	0.087	
Flexor group (2)	M	0.93	0.024	*	0.90	0.037	N.S.
	F	0.86	0.023		0.90	0.055	
Psoas minor (3)	M	1.12	0.135	N.S.	0.77	0.143	*
	F	0.91	0.129		1.29	0.209	
Serratus dors. caud. (4)	M	1.09	0.064	**	0.87	0.098	N.S.
	F	0.85	0.061		1.10	0.144	
Obliq. abdom. intern. (4)	M	1.57	0.034	**	0.95	0.045	N.S.
	F	1.43	0.032		1.00	0.066	
Supraspinatus (5)	M	0.92	0.016	**	0.99	0.034	N.S.
	F	0.99	0.o15		0.91	0.050	
Coracobrachialis (5)	M	0.81	0.047	N.S.	1.12	0.062	*
	F	0.92	0.045		0.84	0.091	
Triceps brachii (5)	M	0.89	0.012	**	0.96	0.021	N.S.
	F	0.94	0.011		0.93	0.032	
Omotransversarius (7)	M	0.77	0.051	N.S.	1.48	0.078	**
	F	0.64	0.049		1.09	0.115	
Latissimus dorsi (8)	M	0.92	0.020	**	1.09	0.038	N.S.
	F	1.00	0.019		1.14	0.055	
Pectoralis prof. + superf. (8)	M	0.94	0.021	*	1.07	0.033	N.S.
	F	1.oo	0.020		1.17	0.049	
Splenius (9)	M	0.89	0.064	N.S.	1.90	0.088	***
	F	0.74	0.061		1.36	0.129	

Table 6.2.7. (continued)

Muscle/group	Sex	Age: 0-16 wks. b	SE	Signific. of diff.	Age: 16-74 wks. b	SE	Signific. of diff.
Longissim. cap. et atlantis (9)	M	0.89	0.079	*	1.59	0.083	**
	F	0.62	0.076		1.18	0.123	
Complexus (9)	M	0.81	0.026	N.S.	1.26	0.043	*
	F	0.75	0.025		1.08	0.063	
Rectus cap. dors. maj (9)	M	0.79	0.067	N.S.	1.15	0.097	*
	F	0.68	0.065		0.79	0.143	
Intraversales colli (9)	M	0.96	0.042	*	1.19	0.056	*
	F	0.83	0.040		0.97	0.082	

B: 16 - 24 wks. and 48 - 74 wks.

Muscle/group	Sex	Age: 16-24 wks. b	SE	Signific. of diff.	Age: 48-74 wks. b	SE	Signific. of diff.
Muscle group 3	M	1.02	0.038	N.S.	1.01	0.114	*
	F	1.04	0.048		0.65	0.117	
Longissimus dorsi (3)	M	1.07	0.058	N.S.	0.94	0.135	N.S.
	F	1.10	0.073		0.71	0.178	
Splenius (9)	M	2.09	0.198	*	1.40	0.175	*
	F	1.47	0.250		0.85	0.195	

Table 6.2.8. Effect of sex on muscle weight distribution at equal ages[x]. (Iceland).

Muscle group	Sex	At birth			20 - 24 wks.			74 wks.		
		% of carc. muscle		Relat. diff.	% of carc. muscle		Relat. diff.	% of carc. muscle		Relat. diff.
		Mean	SE	F=100	Mean	SE	F=100	Mean	SE	F=100
Tot. muscle (wt. in g)	M	1063	N.S. 55.8	116	9355 *	183.4	106	18248 **	836.8	136
	F	914	-		8802	-		13401	-	
Gr. 1 - Prox. hind limb	M	26.0	* 0.32	94	27.2 ***	0.24	93	25.4 ***	0.30	90
	F	27.7	-		29.1	-		28.3	-	
Gr. 2 - Dist. hind limb	M	6.9	N.S. 0.12	97	4.9 **	0.07	95	4.3 +	0.12	92
	F	7.1	-		5.2	-		4.7	-	
Gr. 3 - Around Spin. column	M	13.3	N.S. 0.24	99	15.2 N.S.	0.17	99	14.1 N.S.	0.28	101
	F	13.4	-		15.4	-		14.0	-	
Gr. 4 - Abdominal	M	5.9	N.S. 0.28	108	10.8 N.S.	0.13	102	10.3 N.S.	0.27	96
	F	5.5	-		10.6	-		10.8	-	
Gr. 5 - Prox. fore limb	M	14.4	N.S. 0.25	103	12.0 N.S.	0.10	98	12.9 N.S.	0.20	100
	F	14.0	-		12.2	-		12.8	-	
Gr. 6 - Dist. fore limb	M	5.2	N.S. 0.14	98	3.0 N.S.	0.03	100	3.0 N.S.	0.10	101
	F	5.2	-		3.0	-		2.9	-	
Gr. 7 - Fore limb to neck	M	7.9	N.S. 0.23	108	8.0 *	0.11	104	9.4 **	0.13	109
	F	7.3	-		7.7	-		8.6	-	
Gr. 8 - Fore limb to thorax	M	7.1	* 0.12	111	6.7 N.S.	0.07	102	6.6 +	0.20	91
	F	6.4	-		6.5	-		7.3	-	
Gr. 9 - Neck and thorax	M	13.4	N.S. 0.26	100	12.3 ***	0.16	118	14.0 ***	0.27	133
	F	13.5	-		10.4	-		10.5	-	

'Expensive muscles' (Gr's 1 and 3) at 20 - 24 weeks:

Males: 42.4% (***)

Females: 44.5%

+) $0.05 < p < 0.1$

x) Adjusted for conformation type and type of birth.

capitis et atlantis, which at the highest age comprised 0.67% and 0.62% of total muscle in males, compared with 0.18% and 0.19% in females, respectively. In contrast, the females showed their greatest superiority at the same age with resepct to the muscles semimembranosus and biceps femoris, these constituting 4.89% and 4.75% of total muscle, in comparison to 4.18% and 4.17% in the males, respectively.

6.3. DISCUSSION

a) Common developmental patterns.

Describing individual muscles or muscle groups as either early or late maturing, can lead to confusion of the actual growth patterns, unless the meaning is clearly defined. A common use of these terms implies that the latest maturing muscle would be the one undergoing the greatest relative weight increase from birth to maturity, and vice versa, without a reference to the time in life, during which growth is most intense. On this basis, the abdominal muscles would be described as the latest maturing of all. Nevertheless, their proportional weight gain had been established by 16 weeks of age, after which the relative growth rate of these muscles remained similar to or even lower than the average. Conversely, muscle groups 5, 7, 8 and 9, all of which made considerably lower total relative weight gains over the range studied, had the highest relative growth rates ($b = 1.10 - 1.19$) during the latter phases of development. It thus depends on the definition, whether we describe the abdominal or the neck-thorax muscles as being the latest maturing; however, the classification into impetus groups, over defined age phases, is considered more informative.

The present observed developmental patterns may be summarized in terms of centripetal growth gradients in early life, reaching the greatest intensity in the abdominal region between six and 16 weeks, and later spreading forwards to the thorax and neck. In comparison to earlier works, it is interesting to note that our classification, according to impetus rate, in some respects bears a greater resemblance to that of Butterfield and Berg (1966 b) for cattle, than to either that of Lohse et al. (1971) or Jury et al. (1977) for sheep. Thus Butterfield and Berg detected a decline in the growth impetus of group 4 and an increase in groups 5, 6 and 8, all of which were clssified as

mono-phasic by Jury et al. Conversely, group 3 was described as mono-phasic in the cattle, whereas in sheep, the present study as well as those of Lohse et al. and Jury et al. have clearly demonstrated a high-decreasing impetus pattern.

While we agree with Berg and Butterfield (1976) that the greatest diversity in growth patterns is observed early in life, the present and previous evidence for sheep (Jury et al., 1977) refutes their generalization that after doubling the birth weight of the musculature, all muscles tend to grow at a similar, average impetus rate. Thus most of the muscle groups, and even more so, some individual muscles, were constantly changing their interrelationships throughout the period studied, and more muscles were found to change their impetus patterns around 16 weeks (7-fold muscle birth weight) than at six weeks. We may, however, have missed the peak of diversity, by not killing lambs mid-way between birth and six weeks, by which time the birth weight of the musculature had quadrupled.

The inwards gradient demonstrated in the abdominal region, with the muscle obliqus abdominis internus exhibiting the highest growth intensity of all muscles, can also be seen in the results of Lohse et al. (1971), although not drawn attention to by the authors.

Butterfield (1963 b) opposed the earlier claims of Hammond (1932) and Pálsson (1955) that the lumbar portion of the longissimus dorsi muscle was later maturing than the thoracic part. Our data, from both experiments, supports the earlier workers in clearly demonstrating growth gradients from the cranial and caudal ends of the muscle, terminating in the lumbar section, which constantly increased its proportion of the whole. While this may differ in cattle, the heterogeneous origin of Butterfield's experimental animals may well have confounded the issue.

As remarked before, there was a general tendency for small muscles, closely attached to the skeleton, to grow relatively slower than the larger, more superficial muscles. Pure physical constraint might be postulated as a causative factor; however, Berg and Butterfield (1976) explained this phenomenon by the smaller muscles containing a higher proportion of connective tissue and relatively fewer muscle fibres than the larger muscles. Since the latter type of tissue has a greater potential for growth, it would seem only natural for the

ratio of these constituents to influence the overall growth potential of the muscle.

With respect to the practical implication of differential muscle growth, it is evident that the two most valuable muscle groups (1 and 3) had reached their maximum proportions of total muscle by six weeks of age, or at 6.7 kg carcass weight. From the consumer's point of view, muscle weight distribution deteriorated thereafter. However, the changes in distribution over the commercial range in slaughter age/weight, were relatively small, and it is recommended that lambs should be slaughtered when they are at an optimal level of fatness, commensurate to the consumer's requirements.

b) Genotype effects.

The genotype differences, observed in each trial, cannot be explained in terms of unequal stages of maturity and must be regarded as being the true effects of selection for changes in body form. If the different genotypes were later proved to be identical in mature muscle proportions, then those proportions would have developed along different pathways.

It is of primary interest to note that, while both selection procedures have been associated with proportional changes in the musculature, the effects were not identical. Thus, in Edinburgh, the selection for a short cannon bone has increased the relative amount of loin muscle at the cost of leg muscles, with only minimal effect on the thoracic region. In practical terms an average S-line carcass with 8 kg total muscle would contain 940 g of that muscle in the prime loin and 2930 g in the gigot, compared with 860 g and 3080 g for the L-line, respectively, with C-lambs being intermediate. When combined, the L-line would have an advantage of roughly 1 percentage unit in these two most expensive carcass joints, since their heavier gigot muscle did more than outweight the inferior loin development. By contrast, there was no difference between the L- and S-type in Iceland, regarding gigot muscle, which would suggest that the considerable emphasis placed on the 'fullness of leg' in the selection programme has been fruitful in maintaining a constant proportion of hind leg muscle, despite a relative reduction in leg length. As in Edinburgh, the Icelandic S-type showed superior development of loin muscle, amounting to a difference of 13% or 120 g at 10 kg total muscle weight,

which on the whole gave the S-type a more desirable muscle weight distribution, since this advantage was met in the L-type by a higher proportion of the cheaper thorax and neck muscles. Furthermore, the difference in the loin was mainly found in the longissimus dorsi muscle, the most valuable single muscle in the carcass, which is of particular interest in light of recent findings by Thorsteinsson and Björnsson (1980), who demonstrated a strong negative genetic correlation (-0.62) between cannon bone length and the thickness of that muscle.

c) Sex effects.

The effects of sex on muscle development, demonstrated by the present study, are not markedly dissimilar to those found by Lohse (1973) and Jury et al. (1977). Both reports highlighted the superior male development of the thorax and neck region and, in particular, that of the muscle splenius cervicalis, which was also pointed out in cattle by Brännäng (1971) as the muscle most affected by masculinity.

The increasingly superior development of group 1 muscles in females, with age, is in keeping with Jury et al. (1977), while deviating from the pattern observed by Lohse (1973). Similarly, the present study, as well as Jury et al. (1977) found the impetus rate of group 3 muscles to decline with age to a greater extent in the females, whereas no such effect was observed by Lohse (1973). Perhaps this discrepancy can by explained by the remarkably light weight of Lohse's oldest group of Merino sheep, the two year old rams only weighing 36.1 kg on average and thus, despite the older age, not having achieved the stage of growth, at which the sex difference became most apparent in our data.

Berg and Butterfield (1976) cited evidence for heifers developing a higher proportion of abdominal muscles than bulls and suggested a functional explanation, i.e. a greater abdominal burden due to heavier fat depots, or 'an inbuilt preparation of the female for the advent of pregnancy'. Heap and Lodge (1967) also showed pregnancy to induce growth of the abdominal muscles in sows. While there was no evidence in our data for pregnancy being prepared by the ewes in their first year of life, these had a marginally higher proportion of abdominal muscles (non-significant) in the second autumn. That difference was greatest in the muscle rectus abdominis, (17%, $p < 0.01$) which being most ventr-

ally located, would carry the heaviest burden of pregnancy. More evidence is needed for the question to be resolved

Finally, as relates to the practical aspects of the sexual differences, the females had a significant advantage over males in the combined proportions of muscle groups 1 and 3, or 44.5% compared with 42.4% at 20-24 weeks of age. The corresponding values for heifers and bulls, quoted by Berg and Butterfield (1976), were 43.6% and 40.8%, indicating similar sex effects in cattle to those in sheep.

CHAPTER 7.

DEVELOPMENT OF THE SKELETON

7.1. INTRODUCTION

The development of skeletal proportions has not been studied as widely as that of the musculature. While bone is largely a waste tissue, inpractical terms, and as such of little economic value, the knowledge of its development and particularly of any genetic or environmental variation that may exist is important in relation to the predictive value of the weight or form of individual bones with regard to commercially important carcass features.

Hammond (1932) demonstrated centripetal gradients of increasing growth intensity from the distal to proximal limbs, and an anterio-posterior gradient along the axial skeleton, terminating in the lumbar vertebrae. These findings were substantiated by the works of McMeekan (1940), whth pigs, and Pálsson and Vergès (1952), with sheep, the latter further demonstrating the ribs to have the greatest growth intensity of all skeletal parts in post-natal life. More recently, this pattern of post-natal development has been confirmed by several workers, including in sheep Fourie (1965), in cattle Seebeck and Tulloh (1968), Seebeck (1973 b), Kempster, Cuthbertson and Jones (1977), Jones, Price and Berg (1978) and Berg, Andersen and Liboriussen (1978 d), and in pigs Richmond and Berg (1972), Davies (1975), Goenaga and Carden (1979).

Wallace (1948) had shown with sheep, that those bones growing relatively least after birth had higher specific growth rates in foetal life than the later maturing axial skeleton, ribs or sternum, and a similar pre-natal order was revealed by the radio-graphic study of sheep foetal skeletons by McDonald, Wenham and Robinson (1977).

Hammond (1932) and Fourie (1965) studied in detail the changes in form of individual bones associated with post-natal growth. They showed that both growth in length and thickness of the long bones of the limbs follow the same trend as growth in weight, while the rate of growth in length attains its maximum at an earlier age than thickness growth. Similarly, the scapula and pelvis were found to increase relatively more in width than in length from birth to maturity. In contrast, the skull was shown to grow more in length than in either width or depth, while such patterns varied among the different vertebral types.

Hammond (1932) studied the effects of domestication on skeletal proportions by comparing adult rams of the Suffolk, Soay and Shetland

breeds. He concluded: 'It would appear that those parts of the animal which grow most in postnatal life are those most increased by the changes made by the livestock improver, while the limbs below the carpals and tarsals, parts which grow least in post-natal life, are those which are reduced in proportion.' In accordance with this was the finding by Pålsson (1940) that late maturing breeds had proportionately longer and heavier cannon bones than those which were earlier maturing. Both Hammond (1932) and Pålsson (1940) emphasized the change in the shape of bones associated with breed inprovement, namely the increased thickness relative to length.

More recent studies in sheep (Fourie, 1965) and cattle (Harte and Conniffe, 1967; Seebeck, 1973 b; Truscott, Lang and Tulloh, 1976; Berg et al., 1978 d; Kempster, 1978 and Jones et al., 1978) have demonstrated small but significant differences in bone weight distribution between breeds which, in accordance with the Hammond school's ideas, generally reflect the order of earliness of maturity in the respective breeds. In this context, it is of particular interest to see from the present data whether the selection for cannon bone length within a breed has affected the relative proportions of the rest of the skeleton, or whether the effect has been a uniform one.

Sexual influences on skeletal proportions were studied in sheep by Hammond (1932), Pålsson and Vergés (1952) and Fourie (1965), in cattle by Jones et al. (1978) and in pigs by Richmond and Berg (1972) and Kempster and Evans (1979). Pålsson (1955) summarized these effects in terms of ewes being earlier maturing than rams, hence showing more advanced skeletal development in early life, whereas the rams would ultimately exceed the development of the ewes and thus, at maturity show a higher proportion of the later developing bones than the adult ewes. While, in general, acknowledging this, Fourie (1965) showed the rams to reach the greatest superiority over the ewes in the development of the cervical and thoracic vertebrae, while the ewes attained with age higher proportions in the pelvis and the sacrum. Moreover, Fourie (1965) confirmed the earlier findings of Hammond (1932) that growth in bone thickness was inhibited in the female to a greater extent than growth in length. In cattle, Jones et al. (1978) found growing heifers to show more mature proportions within the skeleton than either steers or bulls, while the two cited pig studies failed to reveal any noticable sex differences in bone weight distribution.

7.2. RESULTS

a) Common developmental patterns.

(i) Weight proportions. The two sets of data were analysed in terms of relative growth coefficients (tables 7.2.1. and 7.2.2.), relating individual bone weights to that of total carcass bone (excluding head and feet). The Icelandic results are further schematically presented as relative weight increases from birth to the various slaughter points (figure 7.2.1.), and for the same data, the changes with age in selected bone weight ratios are shown in table 7.2.3.

In general, the two experiments are in good agreement. All limb bones below the scapula and the pelvis, except the patella, grew relatively slower than the skeleton as a whole. The cannon bones (metacarpals/tarsals) initially exhibited the lowest relative growth rates with growth intensity increasing downwards to the phalanges, and gradually upwards along the limbs, the scapula and pelvis both growing at similar rates and significantly faster than the whole. The patterns were strikingly similar in the fore and hind limbs. The separate analyses of the post-weaning phases revealed slight changes in these patterns, the same in both trials. Thus, the radius and tibia grew at rates similar to or higher than the humerus and femur, respectively, while the carpals and tarsals had fallen in rate below the cannon bones. It is apparent (table 7.2.3.) that the scapula, pelvis and the long bones above the cannon bones continued to increase in proportions relative to the cannon bones throughout the period studied, with the exception of the femur, which showed no rise in proportion after 48 weeks of age. Similarly, the ratios of scapula and pelvis to humerus and femur, respectively, were gradually rising throughout, whereas the ultimate weight relationships between the femur and the tibia and between the humerus and the radius had been established at six and sixteen weeks, respectively. While differential growth rates within the limbs were observed throughout the 74 weeks in the Icelandic study, it is clear that the greatest changes in relative proportions occurred between birth and six weeks of age.

The major bones of the head initially showed the lowest relative growth rates of all bones. In relation to the weight of the spinal column, these fell dramatically in proportion from birth to six weeks. Subsequently, however, the relative growth of these bones accelerated

Table 7.2.1. Relative growth coefficients (b), relating individual bone weights to the weight of total carcass bone. (Edinburgh).

A: Fore limb

Bone	Pre-trial b	Pre-trial SE	On trial b	On trial SE	Signific. of diff.
Scapula	1.11	0.022	1.18	0.037	N.S.
Humerus	0.98	0.022	0.92	0.024	N.S.
Radius-ulna	0.86	0.019	0.96	0.026	*
Carpals	0.93	0.057	0.68	0.096	**
Metacarpus	0.71	0.022	0.81	0.036	*
-----"----+	(0.78-0.62)				

B: Hind limb

Bone	Pre-trial b	Pre-trial SE	On trial b	On trial SE	Signific. of diff.
Pelvis	1.10	0.017	1.16	0.032	N.S.
Femur	0.95	0.013	0.90	0.028	N.S.
Tibia-fibula	0.92	0.031	0.99	0.027	N.S.
Tarsals	0.78	0.123	0.59	0.047	N.S.
Metatarsus	0.70	0.023	0.87	0.037	**
-----"----+	(0.77-0.62)				

C: Trunk

Bone	Pre-trial b	Pre-trial SE	On trial b	On trial SE	Signific. of diff.
Spinal column	1.01	0.015	1.03	0.027	N.S.
Cervical vert.3	0.98	0.021	1.16	0.043	**
Thoracic vert.7	0.96	0.023	0.89	0.042	N.S.
Lumbar vert.4	1.06	0.030	1.08	0.049	N.S.
Ribs 4-6	1.23	0.038	1.22	0.060	N.S.
----"----+	(1.09-1.38)				

+) b-values at 400g and 800g carcass bone weight, respectively.

Table 7.2.2. Relative growth coefficients (b), relating individual bone weights to the weight of total carcass bone[x]. (Iceland).

A: Fore limb

Bone	0 - 16 wks. b	SE	16 - 74 wks. b	SE	Signific. of diff.
Scapula	1.18	0.014	1.06	0.064	N.S.
Humerus	0.92	0.021	0.85	0.065	N.S.
Radius-ulna	0.77	0.012	0.89	0.051	*
Carpals	0.73	0.025	0.55	0.086	*
Metacarpus	0.63	0.014	0.70	0.049	N.S.
Prox.phalanx	0.81	0.020	0.69	0.064	N.S.
Med.phalanx	0.86	0.031	0.62	0.084	*
Dist.phalanx	0.65	0.088	1.08	0.224	N.S.

B: Hind limb

Bone	0 - 16 wks. b	SE	16 - 74 wks. b	SE	Signific. of diff.
Pelvis	1.14	0.013	1.04	0.054	N.S.
Femur	0.90	0.012	0.84	0.047	N.S.
Tibia-fibula	0.82	0.013	0.87	0.045	N.S.
Tarsals	0.69	0.020	0.57	0.067	N.S.
Patella	0.99	0.038	1.02	0.089	N.S.
Metatarsus	0.63	0.017	0.60	0.057	N.S.
Prox.phalanx	0.78	0.026	0.58	0.069	*
Med.phalanx	0.81	0.031	0.60	0.075	*
Dist.phalanx	0.67	0.049	1.07	0.130	**

CONTD.

Table 7.2.2. (continued).

C: Head

Bone	0 - 16 wks. b	SE	16 - 74 wks. b	SE	Signific. of diff.
Skull	0.88	0.043	1.30	0.123	**
---"---+	(0.42-0.95)				
Mandible	0.92	0.041	1.19	0.099	*
---"---+	(0.46-0.98)				
Hyoid bone	0.88	0.049	1.01	0.213	N.S.

D: Trunk

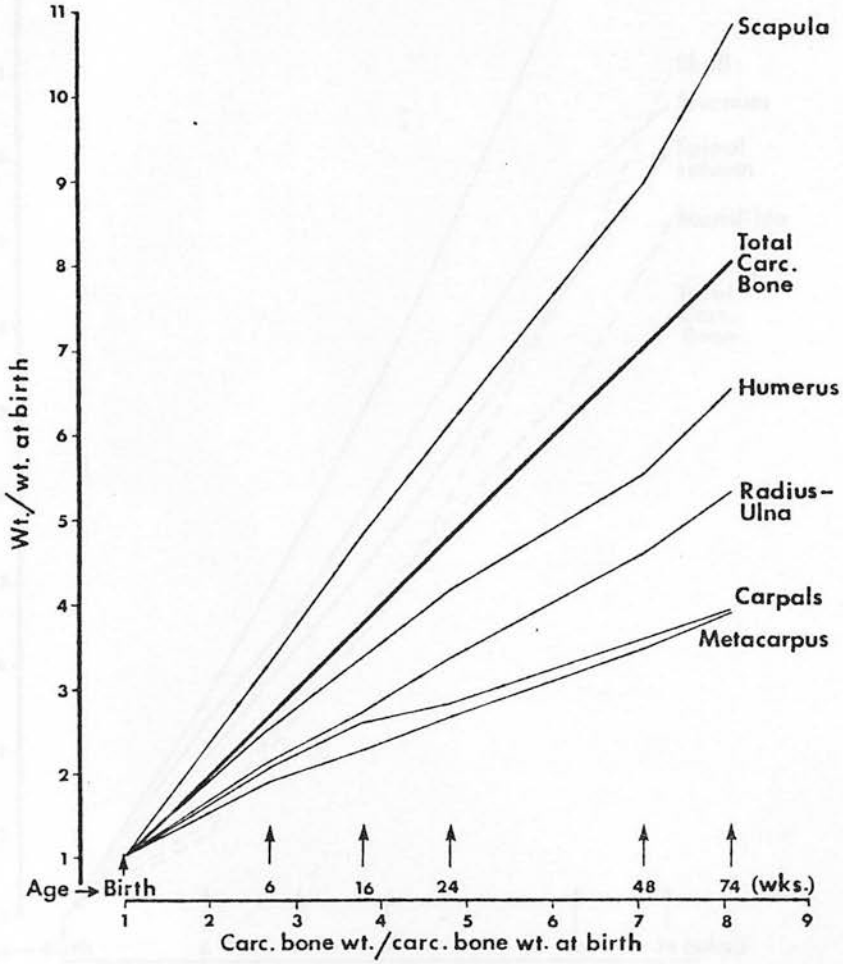
Bone	0 - 16 wks. b	SE	16 - 74 wks. b	SE	Signific. of diff.
Spinal column	1.08	0.010	1.12	0.041	N.S.
Cervical vert.	1.08	0.019	1.24	0.064	*
Thoracic vert.	1.05	0.015	1.10	0.052	N.S.
---"---+	(1.16-1.03)				
Lumbar vert.	1.10	0.020	1.01	0.070	N.S.
Sacral + coccyg vert.	1.09	0.046	1.05	0.110	N.S.
Sternum	1.18	0.029	1.13	0.115	N.S.
Ribs	1.28	0.020	1.14	0.069	N.S.

+) b-values at 400g and 800g carcass bone weight, respectively.

x) Adjusted for conformation type, sex and type of birth.

Figure 7:2:1. RELATIVE GROWTH OF BONES — ICELAND

A: FORE LIMB



B: HIND LIMB

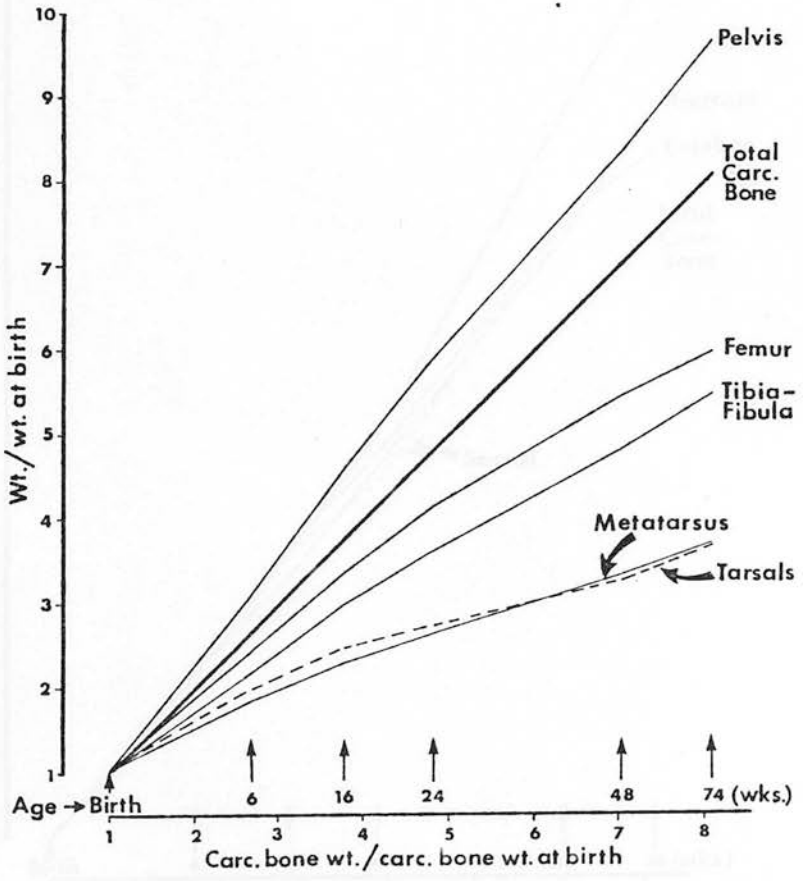


Fig. 7:2:1. Contd.

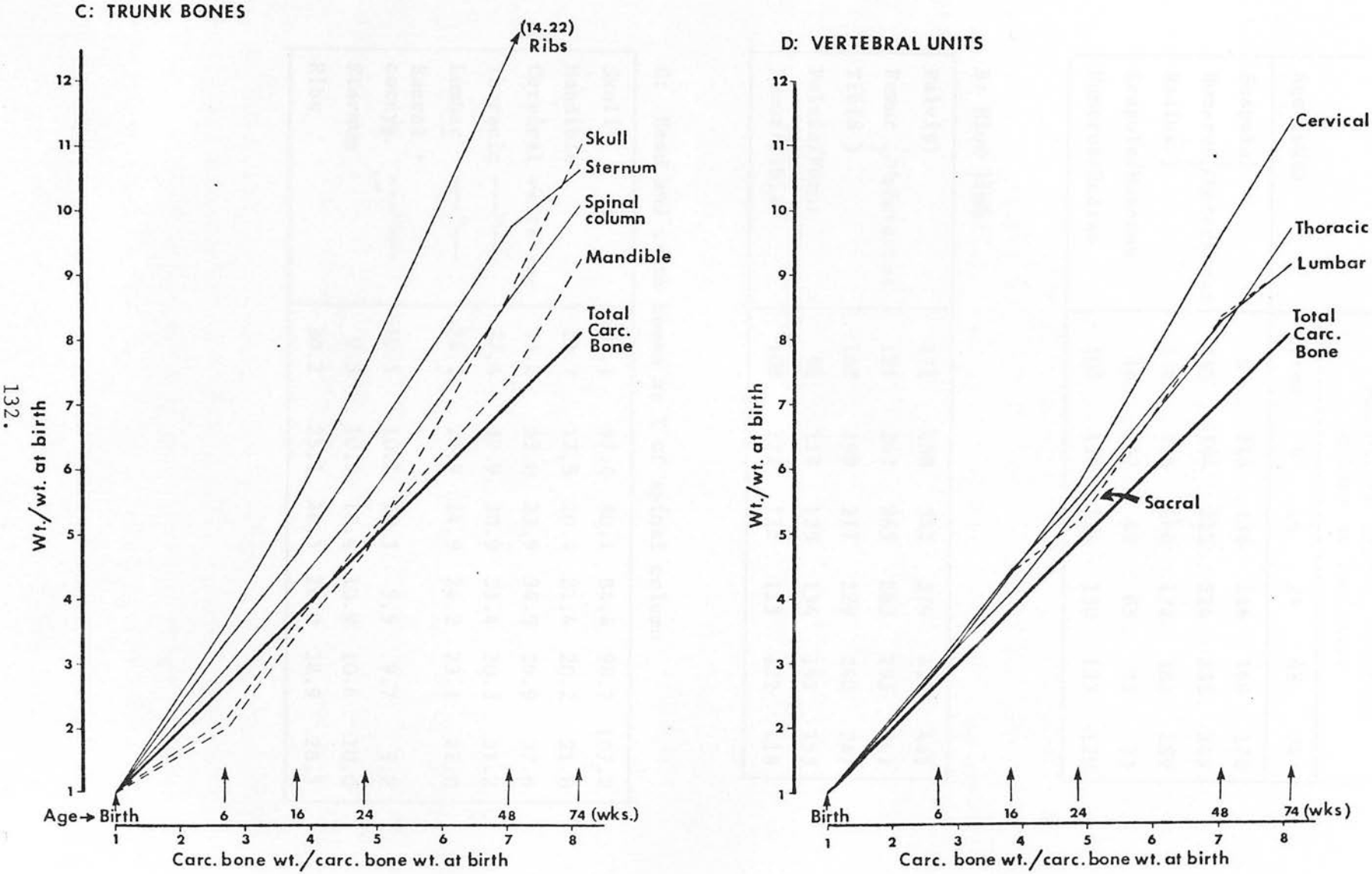


Table 7.2.3. Age changes in weight proportions within the skeleton. (Iceland).

A: Fore limb

Age (wks)	Percentage weight, relative to bone as indicated					
	Birth	6	16	24	48	74
Scapula)	64	111	136	146	166	178
Humerus)/Metacarpus	145	194	215	224	232	243
Radius)	138	154	166	172	183	189
Scapula/Humerus	44	57	63	65	72	73
Humerus/Radius	105	126	130	130	127	129

B: Hind limb

Pelvis)	171	288	342	379	427	445
Femur)/Metatarsus	181	242	265	282	295	291
Tibia)	168	198	217	229	242	247
Pelvis/Femur	94	119	129	134	145	153
Femur/Tibia	108	122	122	123	122	118

C: Head and trunk bones as % of spinal column

Skull	98.1	67.4	80.1	84.4	98.7	107.2
Mandible	23.7	17.5	20.4	21.4	20.2	21.8
Cervical vertebrae	33.2	33.0	33.9	34.9	36.9	37.6
Thoracic ---"---	32.4	32.9	30.9	31.4	30.3	31.2
Lumbar ---"---	24.2	24.9	24.9	24.2	23.1	22.0
Sacral + coccyg. ---"---	10.1	10.1	10.3	9.5	9.7	9.2
Sternum	9.5	10.9	10.4	10.9	10.6	10.0
Ribs	20.2	25.1	26.3	28.0	28.9	28.5

and between 16 and 74 weeks the skull had a higher growth coefficient and increased more in proportion than any other skeletal part. The fact that most of the animals were horned, the cores remaining intact on the skulls, was a major contributing factor to this secondary growth spurt.

The spinal column, as a whole, was close to the average relative growth rate in the Edinburgh sheep, while having a growth coefficient significantly greater than unity in the Icelandic sheep. In both breeds, however, there was a trend towards a rising relative growth rate of this part with increasing age.

Within the spinal column, differential growth patterns were observed. In this regard, however, the two sets of results are not directly comparable, since in Edinburgh only three sample bones (3rd cervical, 7th thoracic, 4th lumbar) were individually weighed and recorded. Of those, the lumbar grew relatively fastest upto weaning ($p < 0.05$), its growth coefficient being 1.06, compared with 0.98 and 0.96 for the cervical and thoracic, respectively. After weaning, the cervical had the highest growth coefficient (1.16), followed by the lumbar (1.08) and the thoracic (0.89), the former two not differing significantly, while both exceeded that of the thoracic vertebra ($p < 0.01$). In Iceland, over the birth - 16 weeks age interval, relative growth rates did not differ significantly between the cervical, thoracic, lumbar and sacral + coccygeal vertebrae. The lumbars, however, had the somewhat highest growth coefficient (1.10) and the thoracic the lowest (1.05), the difference between these two units approaching significance ($p < 0.10$). Over this period the cervicals and the lumbars increased their proportions of the entire column by 0.7 percentage units each, while that of the thoracic vertebrae declined by 1.5 units and the sacrum maintained a constant proportion. Between 16 and 74 weeks, the differential growth patterns were different and more obvious than before. The cervicals now showed the fastest relative growth, having increased their growth coefficient from 1.08 to 1.24 ($p < 0.05$), the corresponding values for the thoracic, lumbar and sacral vertebrae being 1.10, 1.01 and 1.05, respectively. Thus, there was a clear and significant ($p < 0.05$) gradient of declining growth inpetus from the cervical to the lumbar section. The overall effect was reflected in the multiplication of birth weight attained at 74 weeks, this being 11.4, 9.7, 9.2 and 9.1-fold for the four units in

the anterio-posterior order. As will be shown later (part c.), this pattern was influenced by sex, largely by the superior cervical development in the males; nevertheless, a similar, while weaker, trend was apparent in the female sex.

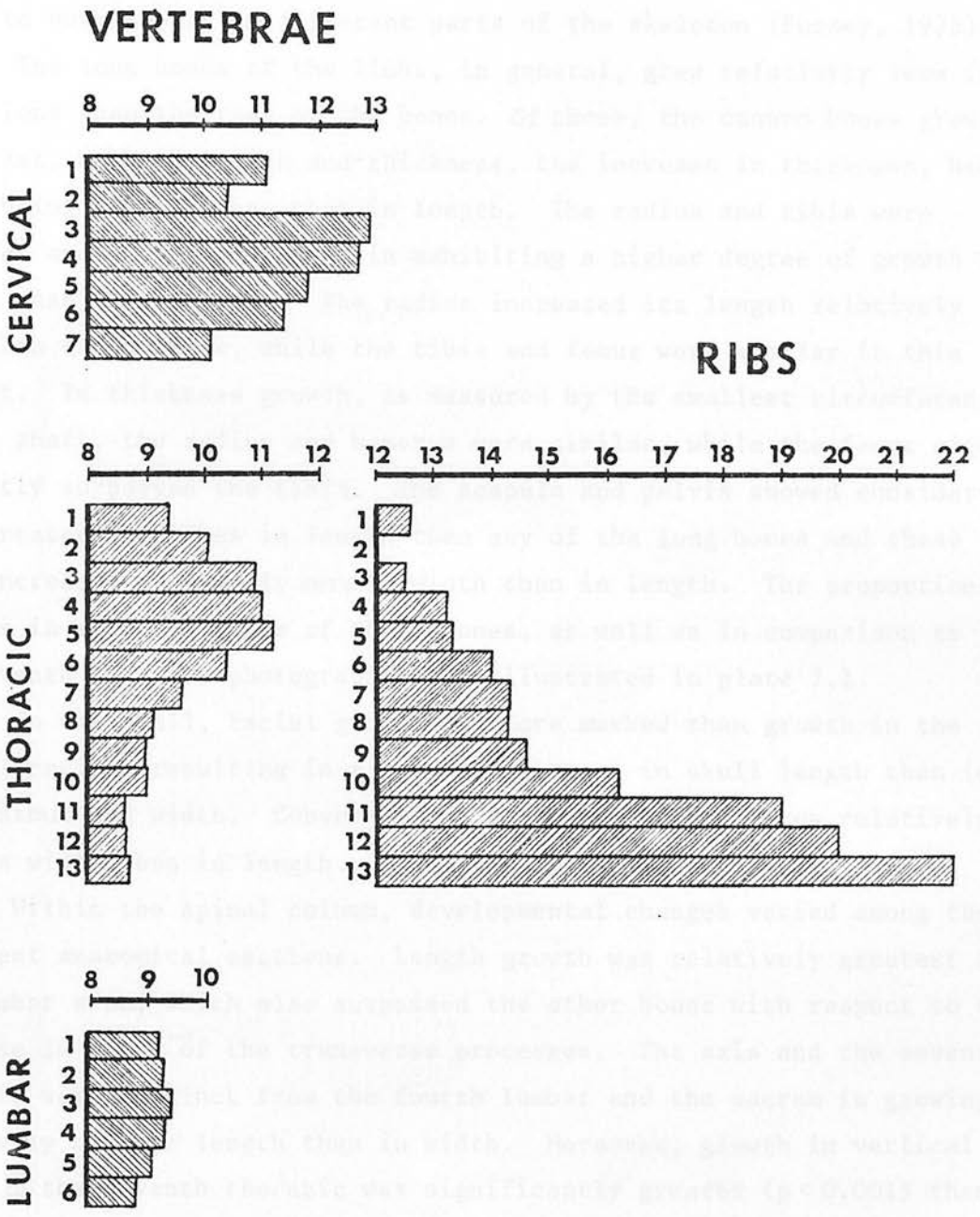
Not only was there differential development among the major anatomical units of the spinal column, but also within them, distinct growth patterns were observed (figure 7.2.2. - see Appendix 14 for relative growth coefficients). These were most apparent, and highly significant in the cervical and thoracic sections, while only just being visible among the lumbar vertebrae. The cervical-thoracic junction can be described as a centre of low activity, in which two separate waves of growth originated. One spread forwards along the neck, reaching a peak and terminating in the third cervical, while the other went backwards, rising to a maximum between the third and the sixth thoracic vertebrae and subsequently dying out. The atlas and axis were distinct among the cervicals in not showing a significant rise in growth rate (relative to the whole spinal column - Appendix 14.) with age and, hence, did not conform to the overall pattern so clearly exhibited by the rest of the cervicals.

The ribs, as a whole, showed the highest relative growth rate of all bones and increased their weight 14.2-fold from birth to 74 weeks, in comparison to the corresponding value of 3.7-fold for the tarsal and metatarsal bones, these showing the smallest relative weight gains after birth. The growth coefficient for the ribs was higher (though not significantly) over the first 16 weeks (1.28) than subsequently (1.14). As within the spinal column, a striking differential growth pattern was found to exist among the ribs (figure 7.2.2). The overall pattern reflects an anterio-posterior gradient of increasing growth impetus, the smallest relative weight gain being attained by the second rib (12-fold) and the largest by the thirteenth rib (22-fold) between birth and 74 weeks of age. It is most interesting to note (Appendix 14.) that the gradient was related to age. Thus, for the first 16 weeks, the growth coefficients with, minor irregularities, gradually rose from the first to the thirteenth rib, while over the subsequent 58 weeks, the lowest activity was observed around the centre, with rising intensity towards both extremes.

(ii) Skeletal dimensions. The relative changes in bone dimensions, associated with age and growth in weight are shown for the Icelandic sheep as

Figure 7.2.2. GROWTH GRADIENTS WITHIN SPINAL COLUMN AND RIBS

—Wt. at 74 wks./ Wt. at birth



relative increases from birth to 74 weeks of age (figure 7.2.3.). Similar patterns were revealed in the Edinburgh data by relating the various bone measurements to total carcass bone weight, or to age, by log-log regressions. In comparing the dimensional changes with those previously described for weight, it is important to bear in mind that none of the measurements are directly indicative of volume; hence no perfect relatonships are to be expected between changes in weight and linear dimensions. Moreover, bone density has not been considered and this is known to vary among the different parts of the skeleton (Fursey, 1975).

The long bones of the limbs, in general, grew relatively less in dimensions than the rest of the bones. Of those, the cannon bones grew the least, both in length and thickness, the increase in thickness, however, being greater than that in length. The radius and tibia were distinct among the limb bones in exhibiting a higher degree of growth in length than in thickness. The radius increased its length relatively more than the humerus, while the tibia and femur were similar in this respect. In thickness growth, as measured by the smallest circumference of the shaft, the radius and humerus were similar, while the femur significantly surpassed the tibia. The scapula and pelvis showed considerably greater increases in length than any of the long bones and these also increased relatively more in width than in length. The proportional changes in size and shape of these bones, as well as in comparison to the seventh rib, are photographically illustrated in plate 7.1.

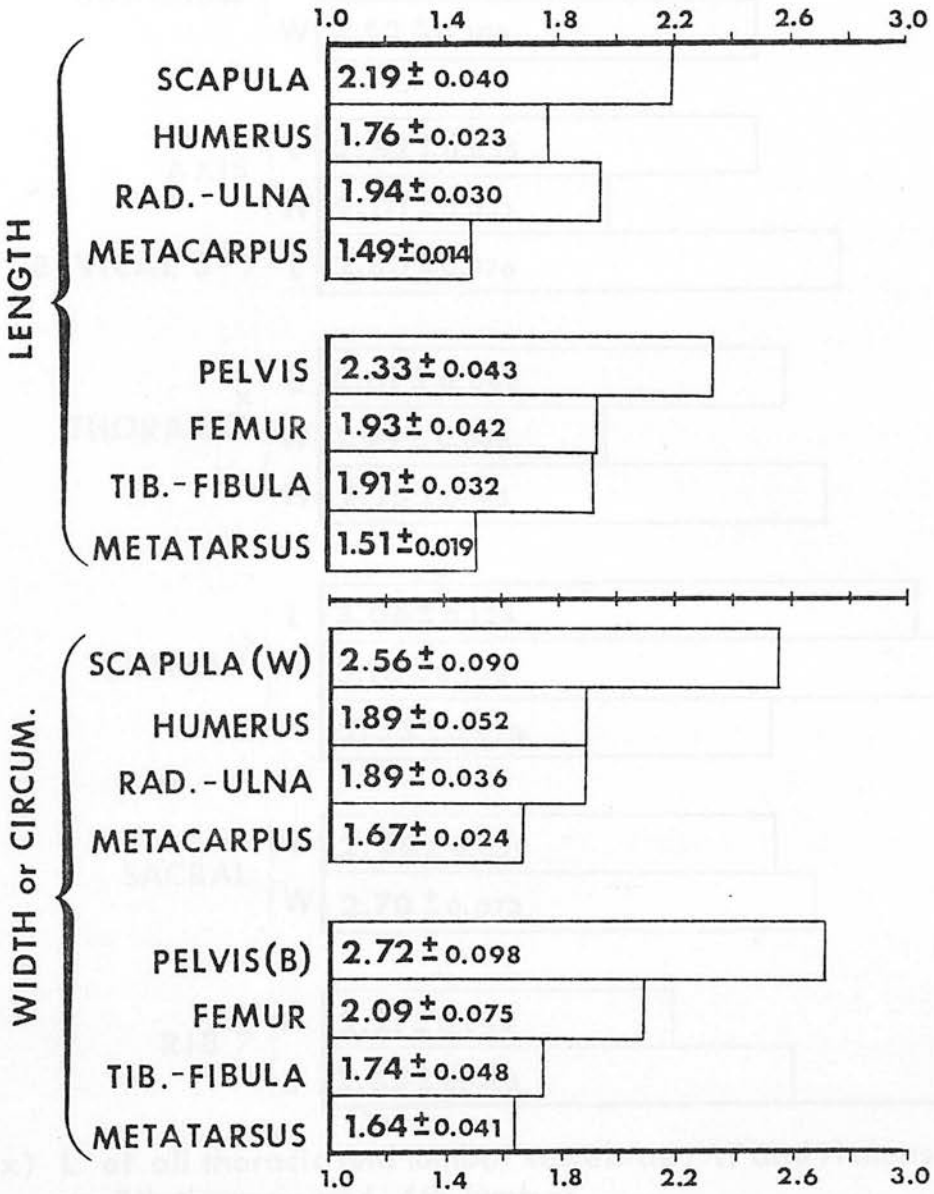
In the skull, facial growth was more marked than growth in the cranial region, resulting in a greater increase in skull length than in the maximum eye width. Conversely, the lower mandible grew relatively more in width than in length.

Within the spinal column, developmental changes varied among the different anatomical sections. Length growth was relatively greatest in the lumbar area, which also surpassed the other bones with respect to the increase in width of the transverse processes. The axis and the seventh thoracic were distinct from the fourth lumbar and the sacrum in growing relatively more in length than in width. Moreover, growth in vertical height of the seventh thoracic was significantly greater ($p < 0.001$) than that in width, whereas the fourth lumbar was increased the most in width and the least in height.

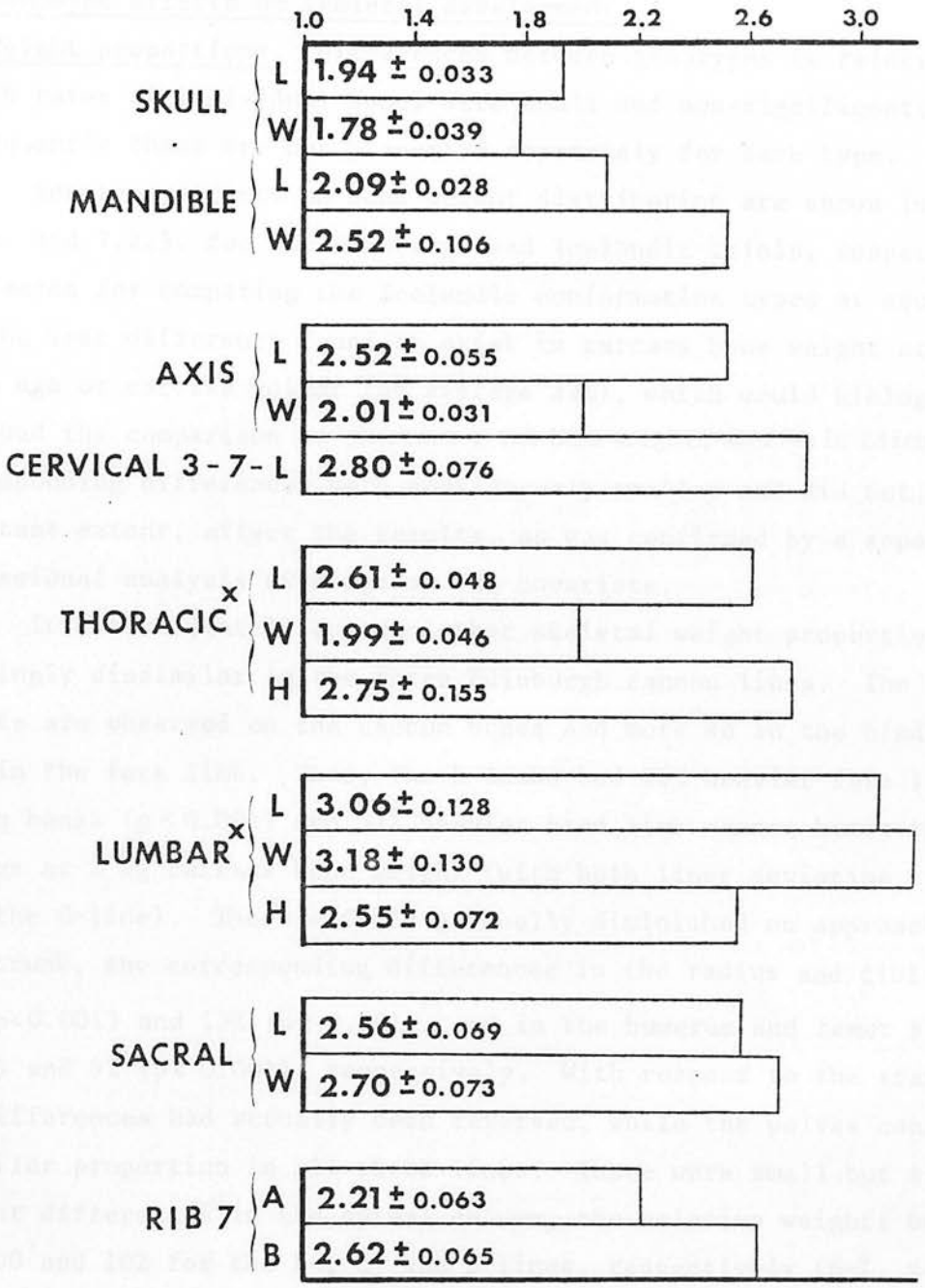
Figure 7.2.3. RELATIVE CHANGES IN SKELETAL DIMENSIONS (ICELAND)

Measurement at 74wks./ Measurement at birth

A. LIMB BONES



B. HEAD AND TRUNK BONES



(x) L of all thoracic and lumbar vertebrae ; W and H measured on 7th thoracic and 4th lumbar

The most significant feature relating to the ribs was the increased spring, relative to the distance between the extreme points, this giving rise to the previously illustrated (Ch. 5.) growth in width relative to depth of the thorax with advancing development.

b) Genotype effects on skeletal development.

(i) Weight proportions. Differences between genotypes in relative growth rates of individual bones were small and non-significant; consequently these are not presented separately for each type.

Genotype effects on bone weight distribution are shown in tables 7.2.4. and 7.2.5. for the Edinburgh and Icelandic trials, respectively. The reason for comparing the Icelandic conformation types at equal ages was the vast difference found to exist in carcass bone weight at any given age or carcass weight (on average 22%), which would biologically confound the comparison at constant total bone weight, whereas in Edinburgh the corresponding differences were considerably smaller and did not, to any important extent, affect the results, as was confirmed by a separate regressional analysis with age as the covariate.

It is immediately apparent that skeletal weight proportions were strikingly dissimilar in the three Edinburgh cannon lines. The greatest effects are observed on the cannon bones and more so in the hind limb than in the fore limb. Thus, the L-lambs had 26% heavier fore limb cannon bones ($p < 0.001$) and 32% heavier hind limb cannon bones than the S-lambs at 2 kg carcass bone weight (with both lines deviating similarly from the C-line). These effects gradually diminished on approaching the body trunk, the corresponding differences in the radius and tibia being 11% ($p<0.001$) and 13% ($p< 0.001$), and in the humerus and femur 8% ($p< 0.001$) and 9% ($p< 0.001$), respectively. With respect to the scapula, the differences had actually been reversed, while the pelvis constitued a similar proportion in all three lines. There were small but significant differences in the spinal column, the relative weights being 97, 100 and 102 for the L-, C- and S-lines, respectively (S-L, $p< 0.01$), and similarly the S-lambs had 7% heavier ribs ($p< 0.01$) than either of the other lines, which were similar.

A different picture emerged from the comparison of the two Icelandic conformation types. It is worth noting that the percentage differences in total carcass bone weight were identical at all three ages for comparison, however, the greater number of animals at 20-24

Table 7.2.4. Effect of cannon line on bone weight distribution[+]. (Edinburgh).

Bone	Line	Carc. bone = 0.8 kg (pre-trial)				Carc. bone = 2.0 kg (On trial)			
		Wt. (g) Mean	SE	% of carcass bone	Relat. diff. (C=100)	Wt. (g) Mean	SE	% of carcass bone	Relat. diff. (C=100)
FORE LIMB									
Scapula	L	20.7	0.6	5.2	95	56.1^{a}	0.6	5.6	94
	C	21.8	0.6	5.5		59.6^{b}	0.6	6.0	
	S	21.6	0.7	5.4	99	60.8^{b}	0.8	6.1	102
Humerus	L	38.7^{a}	1.0	9.7	104	87.6^{a}	0.5	8.8	105
	C	37.3	1.0	9.3		83.3^{b}	0.5	8.3	
	S	35.0^{b}	1.1	8.8	94	80.8^{c}	0.7	8.1	97
Radius-ulna	L	29.5^{a}	0.7	7.4	107	67.0^{a}	0.5	6.7	107
	C	27.5^{b}	0.6	6.9		63.1^{b}	0.5	6.3	
	S	25.4^{c}	0.7	6.4	92	60.4^{c}	0.6	6.0	96
Metacarpus	L	21.2^{a}	0.4	5.3	110	40.0^{a}	0.4	4.0	108
	C	19.2^{b}	0.3	4.8		37.0^{b}	0.4	3.7	
	S	16.8^{c}	0.5	4.2	88	33.0^{c}	0.6	3.3	88
HIND LIMB									
Pelvis	L	54.3	1.2	6.8	100	140.1	1.2	7.0	98
	C	54.5	1.2	6.8		143.0	1.3	7.2	
	S	52.9	1.3	6.6	97	141.5	1.6	7.1	99
Femur	L	48.1^{a}	0.8	12.0	100	112.8^{a}	0.8	11.3	104
	C	48.1^{a}	0.8	12.0		108.6^{b}	0.7	10.9	
	S	45.1^{b}	0.8	11.3	94	103.7^{c}	0.9	10.4	95
Tibia-fibula	L	39.2^{a}	1.4	9.8	104	92.3^{a}	0.6	9.2	106
	C	37.6_{b}	1.5	9.4		87.1^{b}	0.6	8.7	
	S	35.5^{b}	1.6	8.9	95	81.8^{c}	0.8	8.2	94
Metatarsus	L	21.6^{a}	0.4	5.4	112	42.1^{a}	0.5	4.2	109
	C	19.2^{b}	0.4	4.8		38.9^{b}	0.4	3.9	
	S	16.4^{c}	0.5	4.1	85	32.0^{c}	0.6	3.2	84
TRUNK									
Spinal column	L	241.3	4.7	30.0	99	599.2^{a}	6.2	30.0	97
	C	243.2	4.7	30.4		613.8^{b}	4.8	30.7	
	S	249.1	5.5	31.1	102	629.2^{c}	8.5	31.5	102
Ribs 4-6	L	9.4^{a}	0.4	2.4	104	34.2^{a}	0.6	3.4	99
	C	9.0^{a}	0.4	2.3		34.6^{a}	0.6	3.5	
	S	10.6^{b}	0.6	2.7	118	37.1^{b}	0.8	3.7	107

+) Means estimated by regressions and adjusted to constant daily D.M. intake (when on trial).

- Weights refer to bones from one side only (except spinal column and pelvis), the percentages being adjusted accordingly.

Table 7.2.5. Effect of conformation type on bone weight distribution[+]. (Iceland).

Bone	C. type	At Birth			20 - 24 wks.			74 wks.		
		% of carc. bone		Relat. diff. (S=100)	% of carc. bone		Relat. diff. (S=100)	% of carc. bone		Relat. diff. (S=100)
		Mean	SE		Mean	SE		Mean	SE	
Tot. carc. bone (wt. in g)	L	404	+ 21.8	122	1976	*** 22.2	122	3288	* 171.6	122
	S	331	-		1617	-		2686	-	
FORE LIMB										
Scapula	L	4.3	N.S. 0.15	93	5.7	N.S. 0.09	98	5.8	* 0.11	92
	S	4.6	-		5.8	-		6.3	-	
Humerus	L	10.3	N.S. 0.14	103	8.7	N.S. 0.09	98	8.2	N.S. 0.18	99
	S	10.0	-		8.9	-		8.4	-	
Radius-ulna	L	9.7	N.S. 0.13	102	6.7	N.S. 0.08	97	6.4	N.S. 0.15	98
	S	9.5	-		6.9	-		6.5	-	
Metacarpus	L	7.5	** 0.18	114	4.0	** 0.04	105	3.4	N.S. 0.07	100
	S	6.6	-.		3.8	-		3.4	-	
HIND LIMB										
Pelvis	L	6.3	N.S. 0.11	103	7.7	N.S. 0.07	102	7.5	N.S. 0.19	98
	S	6.1	-		7.6	-		7.6	-	
Femur	L	13.5	N.S. 0.28	104	11.2	N.S. 0.14	97	9.8	N.S. 0.20	100
	S	13.0	-		11.5	-		9.8	-	
Tibia-fibula	L	12.6	N.S. 0.28	106	9.2	N.S. 0.11	99	8.5	N.S. 0.18	104
	S	11.9	-		9.3	-		8.2	-	
Metatarsus	L	7.5	N.S. 0.28	107	4.0	N.S. 0.05	100	3.5	N.S. 0.08	102
	S	7.1	-		4.0	-		3.4	-	
HEAD										
Skull	L	23.4	N.S. 1.06	94	22.0	N.S. 0.71	92	29.2	N.S. 1.14	92
	S	24.9	-		23.9	-		31.7	-	
Mandible	L	5.5	N.S. 0.34	86	5.5	* 0.12	92	6.4	N.S. 0.30	89
	S	6.4	-		5.9	-		7.2	-	

CONTD.

Table 7.2.5 (continued).

Bone	C. type	At Birth		20 - 24 wks.		74 wks.	
		% of carc. bone	Relat. diff. (S=100)	% of carc. bone	Relat. diff. (S=100)	% of carc. bone	Relat. diff. (S=100)
TRUNK							
Spinal column	L	24.1	N.S. 0.56	27.7	N.S. 0.27	30.1	N.S. 0.71
	S	24.3	-	27.0	-	28.8	-
			99		103		104
Cervical vert.	L	8.1	N.S. 0.20	9.6	N.S. 0.14	11.2	N.S. 0.29
	S	8.0	-	9.3	-	10.6	-
			101		103		105
Thoracic vert.	L	7.8	N.S. 0.19	8.8	N.S. 0.10	9.3	N.S. 0.15
	S	7.8	-	8.5	-	9.0	-
			100		103		103
Lumbar vert.	L	5.8	N.S. 0.16	6.7	N.S. 0.10	6.7	N.S. 0.21
	S	5.9	-	6.5	-	6.5	-
			98		103		104
Sacral vert.	L	2.4	N.S. 0.14	2.7	N.S. 0.06	2.9	N.S. 0.14
	S	2.5	-	2.6	-	2.7	-
			96		102		108
Sternum	L	1.9	* 0.12	3.1	N.S. 0.09	3.1	N.S. 0.11
	S	2.5	-	2.9	-	2.9	-
			77		104		108
Ribs	L	9.4	N.S. 0.19	15.2	N.S. 0.23	16.7	N.S. 0.57
	S	10.0	-	15.2	-	17.5	-
			95		101		95

+) Adjusted for sex and type of birth.

weeks (16 of each type) than either at birth or 74 weeks (4 of each type) makes that comparison least prone to the effect of individuality and thus most reliable.

The only significant effects within the limbs were those on the fore cannon bone and the scapula. Proportionately, the fore cannon bone was 14% ($p < 0.01$) heavier in the L-lambs at birth and 5% ($p < 0.01$) at 20-24 weeks, whereas at 74 weeks the fore cannon bone constituted an equal proportion of the whole in both types. This gradual change was a reflection of a marginally higher relative growth rate of this bone in the S-lambs. The scapula tended to weigh relatively more in the S-lambs; however, only significantly so in the oldest group. In direct contrast with the Edinburgh study, the overall impression from the Icelandic results is one of a striking similarity in the weight relationships of the limb bones, to the rest of the skeleton in the two different conformation types.

The S-type showed somewhat higher proportions of the head bones than L-type. However, this was only significant for the lower mandible (8%, $p < 0.05$) at 20-24 weeks. The apparent type effect on the proportional skull weight (while non-significant) partly resulted from an element of polledness in the L-type which often produced lambs with intermediary horn growth.

Apart from the signficant effect on the sternum at birth ($p < 0.05$) the rest of the major skeletal units in the trunk were fairly similar in both types, though the vertebral column tended to make up a marginally higher proportion of the whole in the L-type.

(ii) Skeletal dimensions. The various bone measurements are compared in the Edinburgh sheep at constant total carcass bone weight (table 7.2.6.), having found this to yield the same results as if the comparison were undertaken at constant age.

With respect to the length measurements of the limb bones, the ranking of the cannon lines is the same as in the previous weight comparison. Similarly too, the greatest relative differences were found in the cannon bones and more so in the hind than in the fore cannon bones, i.e. 34% ($p < 0.001$) and 29% ($p < 0.001$), respectively between the L- and S-lines. The corresponding differences were considerably smaller, 8-10% ($p < 0.01 - 0.001$) in the other long bones, while still smallest with respect to the scapula and the pelvis (4%, $p < 0.001$). The ranking in

Table 7.2.6. Effect of cannon line on skeletal dimensions.[+] (Edinburgh).

Bone	Line	Length (mm) Mean	SE	Relat. diff. (C=100)	Width (mm)[++] Mean	SE	Relat. diff. (C=100)
A: Limb bones.							
Scapula	L	132.7[a]	0.74	102	94.4[a]	0.64	96
	C	130.3[b]	0.76		98.4[b]	0.70	
	S	127.1[c]	0.98	98	97.3[b]	0.92	99
Humerus	L	125.9[a]	0.48	107	55.3[a]	0.36	100
	C	117.8[b]	0.47		55.3[a]	0.38	
	S	115.1[c]	0.61	98	57.5[b]	0.52	104
Radius-ulna	L	190.1[a]	0.92	105	48.4	0.57	102
	C	180.7[b]	0.92		47.4	0.58	
	S	173.8[c]	1.17	96	47.5	0.76	100
Metacarpus	L	127.4[a]	0.72	112	44.8[a]	0.27	98
	C	113.8[b]	0.68		45.9[b]	0.29	
	S	98.6[c]	0.78	87	47.4[c]	0.40	103
Pelvis	L	182.8[a]	0.94	102	137.4[a]	1.42	96
	C	179.1[b]	0.97		143.5[b]	1.56	
	S	175.4[c]	1.25	98	139.6	2.01	97
Femur	L	159.2[a]	0.78	106	56.2	0.41	99
	C	150.3[b]	0.78		56.9	0.44	
	S	146.2[c]	1.00	97	55.7	0.57	98
Tibia-fibula	L	199.5[a]	1.40	106	47.2	0.33	101
	C	188.8[b]	1.39		46.9	0.35	
	S	181.4[c]	1.76	96	46.3	0.46	99
Metatarsus	L	134.3[a]	0.88	111	43.8[a]	0.27	99
	C	120.5[b]	0.88		44.2	0.29	
	S	100.2[c]	0.91	83	44.9[b]	0.35	102
B: Trunk bones.							
Axis	L	57.0	0.38	101	46.0[a]	0.26	105
	C	56.5	0.39		44.0[b]	0.26	
	S	56.0	0.52	99	43.6[b]	0.35	99
Thoracic vert., 7th.	L	19.8	0.39	102	38.1	0.51	100
	C	19.5	0.41		38.0	0.54	
	S	19.9	0.55	102	37.7	0.71	99

Table 7.2.6. (continued)

Bone	Line	Length (mm)			Width (mm)++		
		Mean	SE	Relat. diff. (C=100)	Mean	SE	Relat. diff. (C=100)
B: Trunk bones.							
Lumbar vert., 4th.	L	31.0	0.12	101	94.6	0.67	99
	C	30.8	0.17		95.5[a]	0.71	
	S	31.0	0.18	101	92.9[b]	0.91	97
Rib, 7th.	L	160.0[a]	1.27	101	43.7[a]	0.54	104
	C	158.5	1.32		42.2	0.55	
	S	155.7[b]	1.71	98	41.3[b]	0.71	98

+) Estimated by regressions on total carcass bone weight = 2.0 kg and adjusted to constant daily D.M. intake.

++) Smallest circumference on the long limb bones and spring (B) on the rib.

regard to bone thickness was the reverse for the cannon bones, the differences between S- and L-lambs being 6% ($p < 0.001$) and 3% ($p < 0.05$) in the smallest circumference of the fore and hind cannons, respectively. As for other criteria of shape, the S-line fore cannon bones were characterized by a flattened shaft with broad but relatively thin extremeties, while those from the L-line were more round in shape. Similarly, the S-lambs showed increased thickness of the humerus, compared with the other two lines ($p < 0.01$), while the scapula was significantly ($p < 0.05$) broader in S- and C-lambs than in the L-lambs. While the absolute measurements of circumference of the radius, tibia and femur did not differ significantly between lines, the ratio of thickness to length was highest in the S-line and lowest in the L-line (see illustrations in plate 7.2.)

The measurements recorded of vertebrae and ribs (including seven additional measurements not reported here) did not reveal any outstanding line effects on either size or shape. Considerable variation was observed in lumbar shape, especially with respect to the vertical, as well as horizontal angles of the transverse processes to the vertebral body; this however, we have failed to identify as a characteristic cannon line effect.

A most striking observation was made with respect to irregularities in the number of vertebrae within the different sections of the spinal column (table 7.2.7). While all the lambs had seven cervicals, the thoracic number varied from 12 to 14, and lumbar vertebrae were either six or seven. Only two lambs had 12 thoracic, one an L-lamb, the other a C-lamb. Of ten lambs with 14 thoracic, eight were C-lambs and two S-lambs. The outstanding feature relates to the apparent selectional effect on the frequency of seven lumbar vertebrae. While overall, 37.3% of the lambs had seven lumbars, the incidence was highest in the S-line, i.e. 62.5% compared with 40.0% and 15.9% in the C- and L-lambs, respectively. This line effect was highly significant ($p < 0.01$) as judged in a Chi-squared test. It is noteworthy, that none of the lambs with 14 thoracic vertebrae had seven lumbars.

In contrast to the Edinburgh results, it is apparent (table 7.2.8. -plate 7.3.) that conformation type effects in Iceland were far more uniform thoughout the skeleton, which is consistent with the observed weight proportions. Thus, all the bones measured were significantly

Table 7.2.7. Effect of cannon line on the number of thoracic and lumbar vertebrae. (Edinburgh).

Line	L	C	S	All
No. of lambs dissected	44	50	32	126
No. with 12 thoracic	1 (2.3)	1 (2.0)	0 (0.0)	2 (1.6)
" " 13 "	43 (97.7)	41 (82.0)	30 (93.8)	114 (90.5)
" " 14 "	0 (0.0)	8 (16.0)	2 (6.2)	10 (7.9)
No. with 6 lumbar	37 (84.1)	30 (60.0)	12 (37.5)	79 (62.7)
" " 7 "	7 (15.9)	20 (40.0)	20 (62.5)	47 (37.3)

For frequency of 7 lumbars: $\chi^2 = 10.93$, $p < 0.01$. (Percentages in brackets)

greater in dimensions, both length and circumference or width, in the L-type than in the S-type. These differences were only marginally greater in the limb bones than in the axial skeleton, with an apparent tendency for the cannon bones to differ the most in length. As in Edinburgh, the S-type was characterized by greater thickness, relative to length, of all the long limb bones and further by the flattened shaft and refined extremeties of the fore cannon bone. The shape of the seventh rib was also markedly different in the two types. The L-type had longer ribs (12%, $p < 0.001$) with relatively less spring, this being associated with the deeper and narrower thorax, described earlier (Ch.5.)

The number of vertebrae showed little variation from the regular pattern: 7-13-6, for cervical, thoracic and lumbar vertebrae, respectively. Two L-type lambs had 12 thoracic and seven lumbars and one L-lamb had 12-thoracic and six lumbars, no other irregularities being found.

c) Influence of sex on skeletal development.

(i) Weight proportions. The relative growth rates of six individual bones or skeletal units were significantly affected by sex (table 7.2.9). These effects were reflected in differential age changes in weight proportions within the skeleton, which are shown in table 7.2.10.

There were no significant differences between the two sexes in the proportional weights of individual bones at birth; however, such differences emerged with age. The differential age changes were gradual and consistent throughout the period of study. Thus, the effects of sex

Table 7.2.8. Effect of conformation type on skeletal dimensions[+]. (Iceland).

Bone	Type	Length (mm)			Width (mm)[x]		
		Mean	SE	Relat. diff. (S=100)	Mean	SE	Relat. diff. (S=100)
A: Limb bones							
Scapula	L	134.3***	0.82	113	89.9***	0.94	109
	S	119.0	-		82.6	-	
Humerus	L	125.2***	0.67	111	52.5***	0.49	105
	S	112.6	-		49.8	-	
Radius-ulna	L	185.4***	0.94	111	45.9***	0.36	105
	S	166.7	-		43.8	-	
Metacarpus	L	125.3***	0.64	115	45.6*	0.58	105
	S	108.8	-		43.4	-	
Pelvis	L	175.6***	1.25	112	133.9***	0.92	105
	S	156.7	-		127.9	-	
Femur	L	158.1***	0.91	110	56.6**	0.66	105
	S	144.0	-		53.7	-	
Tibia-fibula	L	198.6***	1.12	112	47.3**	0.62	108
	S	177.4	-		43.8	-	
Metatarsus	L	130.8***	0.83	113	44.2**	0.54	105
	S	115.9	-		42.0	-	
B: Trunk bones							
Axis	L	54.3***	0.42	107	44.2**	0.42	104
	S	50.9	-		42.5	-	
Thoracic vert.[xx]	L	20.7***	0.15	107	40.1***	0.41	113
	S	19.3	-		35.5	-	
Lumbar vert.[xx]	L	29.9***	0.25	108	90.8***	0.68	105
	S	27.7	-		86.5	-	
Rib, 7 th.	L	171.6***	1.04	112	38.1N.S.	0.36	99
	S	153.9	-		38.5	-	

+) Means of 16, 20 and 24 weeks slaughter groups, adjusted for sex and type of birth.

x) Smallest circumference of the long limb bones.

xx) Mean length of single vertebrae and width of the 7th thoracic and the 4th lumbar vertebra, respectively.

were greatest in the oldest slaughter group, at which time the males had the most superior relative development of the skull (83%, $p < 0.001$), the cervical (31%, $p < 0.001$) and the thoracic vertebrae (21%, $p < 0.001$).

Table 7.2.9. Effect of sex on relative growth rates of bones.+ (Iceland)

Bone	Sex	Birth-16 wks. b	SE	Signific. of diff.	16-74 wks. b	SE	Signific. of diff.
Scapula	M	1.15	0.019	*	1.06	0.066	N.S.
	F	1.21	0.021		1.05	0.072	
Pelvis	M	1.14	0.018	N.S.	1.00	0.056	*
	F	1.13	0.018		1.09	0.061	
Mandible	M	0.92	0.056	N.S.	1.04	0.102	***
	F	0.92	0.058		1.33	0.111	
Cervical vertebrae	M	1.14	0.025	**	1.23	0.066	N.S.
	F	1.02	0.026		1.25	0.072	
Spinal comumn	M	1.10	0.014	*	1.14	0.043	N.S.
	F	1.06	0.014		1.11	0.047	

+) Bone weight related to total carcass bone weitht.

Conversely, at 74 weeks, the early maturing long bones of the limbs as well as the pelvis, sacrum and the lower mandible, made up higher proportions (6-27%) in the females than in the males while the lumbar vertebrae and ribs did not differ significantly in proportions between the sexes at any stage of development.

(ii) Skeletal dimensions. Sex differences in linear dimensions (table 7.2.11) were generally small at early stages of growth, but increased with age as a result of the more prolonged growth in the males. At 74 weeks, all the bones measured were greater in size in the males; though not uniformly so. Thus, with the exception of the femur, differences in the long limb bones were greater in thickness than in length. The pelvis was similar in length in both sexes at 20-24 weeks, while being significantly wider in the females, particularly so at the tuber ischii (11%, $p<0.001$). While at 74 weeks, the differences in pelvis measurements were nonsignificant (only 4 animals of each sex), the male pelvis was now both longer (4%) and wider at the tuber coxae, whereas the width at the

Table 7.2.10. Effect of sex on bone weight distribution.+ (Iceland).

Bone	Sex	AT BIRTH % of carc. bone		Relat. diff. (F=100)	20-24 wks. % of carc. bone		Relat. diff. (F=100)	74 wks. % of carc. bone		Relat. diff. (F=100)
Tot. carc. bone (Wt. in g)	M	382	N.S. 21.8	108	1855	*** 22.1	107	3602	** 171.6	152
	F	353	-		1737	-		2372	-	
FORE LIMB										
Scapula	M	4.6	N.S. 0.15	105	5.7	N.S. 0.09	99	6.0	N.S. 0.11	99
	F	4.4	-		5.8	-		6.1	-	
Humerus	M	10.1	N.S. 0.14	99	8.8	N.S. 0.10	99	8.0	* 0.18	93
	F	10.2	-		8.9	-		8.6	-	
Radius-ulna	M	9.6	N.S. 0.13	99	6.7	N.S. 0.09	99	6.2	N.S. 0.15	94
	F	9.7	-		6.8	-		6.6	-	
Metacarpus	M	7.1	N.S. 0.18	101	3.9	N.S. 0.04	100	3.3	* 0.07	91
	F	7.0	-		3.9	-		3.6	-	
HIND LIMB										
Pelvis	M	6.3	N.S. 0.11	102	7.5	** 0.08	96	7.1	* 0.19	89
	F	6.1	-		7.8	-		7.9	-	
Femur	M	13.1	N.S. 0.28	98	11.2	N.S. 0.14	98	9.2	** 0.20	88
	F	13.3	-		11.4	-		10.5	-	
Fibia-fibula	M	12.0	N.S. 0.28	97	9.1	N.S. 0.10	96	7.8	** 0.18	89
	F	12.4	-		9.5	-		8.8	-	
Metatarsus	M	7.5	N.S. 0.28	105	4.0	N.S. 0.05	100	3.1	** 0.08	84
	F	7.1	-		4.0	-		3.7	-	
HEAD										
Skull	M	25.0	N.S. 1.06	107	27.0	*** 0.69	143	39.4	*** 1.14	183
	F	23.4	-		18.8	-		21.5	-	
Mandible	M	5.7	N.S. 0.34	92	5.6	N.S. 0.12	96	6.0	* 0.30	78
	F	6.2	-		5.8	-		7.6	-	
TRUNK										
Spinal column	M	24.2	N.S. 0.56	100	28.2	*** 0.22	106	31.7	** 0.72	116
	F	24.2	-		26.5	-		27.3	-	
Cervical vert.	M	8.0	N.S. 0.20	100	10.1	*** 0.14	115	12.4	*** 0.29	131
	F	8.1	-		8.8	-		9.5	-	

Table 7.2.10. (continued)

Bone	Sex	AT BIRTH			20-24 wks.			74 wks.		
		% of carc. bone		Relat. diff. (F=100)	% of carc. bone		Relat. diff. (F=100)	% of carc. bone		Relat. diff. (F=100)
TRUNK (continued)										
Thoracic vert.	M	7.9	N.S. 0.19	103	8.9	*** 0.09	103	10.0	*** 0.15	121
	F	7.7	-		8.4	-		8.3	-	
Lumbar vert.	M	5.7	N.S. 0.16	95	6.7	N.S. 0.09	103	6.6	N.S. 0.21	101
	F	6.0	-		6.5	-		6.5	-	
Sacral vert.	M	2.5	N.S. 0.14	106	2.5	*** 0.05	90	2.6	N.S. 0.14	90
	F	2.4	-		2.8	-		2.9	-	
Sternum	M	2.3	N.S. 0.12	108	2.9	N.S. 0.08	96	2.9	N.S. 0.11	91
	F	2.2	-		3.1	-		3.2	-	
Ribs	M	9.7	N.S. 0.19	101	15.0	N.S. 0.22	98	17.3	N.S. 0.57	103
	F	9.7	-		15.3	-		16.8	-	

+) Adjusted for conformation type and type of birth.

Table 7.2.11. Effect of sex on skeletal dimensions.+ (Iceland).

Males as percentage of females.

Age		Birth		20-24 wks.		74 wks.	
A: Fore limb.							
Scapula	L	100	N.S.	100	N.S.	112	*
	W	94	N.S.	101	N.S.	103	N.S.
Humerus	L	101	N.S.	100	N.S.	108	**
	C	105	N.S.	105	**	110	*
Radius-ulna	L	101	N.S.	101	N.S.	109	*
	C	103	N.S.	103	N.S.	113	*
Metacarpus	L	101	N.S.	100	N.S.	106	*
	C	109	**	102	N.S.	110	*
B: Hind limb.							
Pelvis	A	100	N.S.	98	N.S.	104	N.S.
	B	107	N.S.	96	**	106	N.S.
	G	94	*	88	***	90	N.S.
Femur	L	103	N.S.	100	N.S.	110	*
	C	101	N.S.	99	N.S.	106	N.S.
Tibia-fibula	L	100	N.S.	100	N.S.	106	N.S.
	C	102	N.S.	103	N.S.	111	*
Metatarsus	L	102	N.S.	101	N.S.	106	*
	C	108	N.S.	100	N.S.	108	*
C: Head.							
Skull	L	103	N.S.	103	**	108	*
	W	96	N.S.	102	N.S.	105	N.S.
Mandible	L	100	N.S.	102	N.S.	107	*
	W	107	N.S.	101	N.S.	112	*
D: Trunk.							
Axis	L	103	N.S.	105	***	105	N.S.
	W	102	N.S	106	***	118	***
Thoracic, 7th.	L	100	N.S.	101	N.S.	110	*
	W	102	N.S.	103	N.S.	113	**
Lumbar, 4th.	L	100	N.S.	101	N.S.	109	*
	W	101	N.S.	99		106	N.S.
Sacrum	L	100	N.S.	101	N.S.	107	N.S.
	W	103	N.S.	94	**	99	N.S.
Rib, 7th.	A	96	N.S.	100	N.S.	104	N.S.
	B	111	N.S.	96	N.S.	111	N.S.

+) Adjusted for conformation type & type of birth.

tuber ischii was still 10% greater in the females. It should be emphasized that at this age, total carcass bone was 52% heavier and the pelvis 36% heavier in the males than in the females and that the comparison of measurements is made in absolute terms.

The sacrum and the scapula were relatively shorter and wider in shape in the females. Conversely, the significant feature of the axis was its greater width in the males (18%, $p < 0.001$), while no outstanding effects were observed with respect to thoracic or lumbar shapes.

7.3. DISCUSSION

a) Common developmental patterns.

In accordance with earlier works (Pålsson, 1955; Fourie, 1965), the present study has revealed marked differential growth patterns within the skeleton in post-natal life. Evidently, however, the post-natal changes in skeletal proportions were relatively smaller than those observed in the musculature, a high degree of differentiation already having taken place pre-partum (Wallace, 1948). While the developmental changes were most rapid in early life, and certain bones did not alter in proportions, relative to one another, after six weeks of age, differential growth patterns were still observed, in each trial, throughout the period of study.

The gradients established within the limbs are in firm agreement with earlier findings (Hammond, 1932; Pålsson and Vergés, 1952; Fourie, 1965), and similarly, the whole spinal column, sternum and ribs conformed to the relative order demonstrated by Pålsson and Vergés (1952) and Fourie (1965). The proportional weight increase of the skull in the Icelandic sheep was substantially greater than found by Fourie (1965); this however, is readily explained by the former breed being predominantly horned, while Fourie's sheep were all polled.

The one area of controversy, resulting from the present study, concerns the development of the axial skeleton. Whereas Hammond (1932) and Pålsson and Vergés (1952) found the lumbar section to increase relatively most, in weight, after birth, a different pattern has been revealed in the Icelandic sheep, the growth intensity being lowest in the lumbar and sacral parts, intermediate in the thorax and highest in the cervical vertebrae. Fourie (1965) also observed the greatest relative growth in the cervicals; however, in his case growth was least

active in the thoracic vertebrae, which was also apparent in Hammond's (1932) data, and would further appear to be indicated by the present Edinburgh results.

In an attempt to explain this discrepancy a comparison of the Icelandic results with those of Fourie (1965) is presented in table 7.3.1.

Table 7.3.1. Effect of sex on the relative weight increase of the skull and the different vertebral parts.

Bone	Sex	I: Icelandic results		II. Fourie (1965)		I/II %
		74 wks./ Birth	Relat. diff. (F=100)	80 wks./ Birth	Relat. diff. (F=100)	
Total carcass bone	M	9.43	141	7.01	125	135
	F	6.71		5.59		120
Skull	M	15.39	249	7.00	130	220
	F	6.17		5.38		115
Cervical	M	14.71	186	9.12	140	161
	F	7.91		6.51		122
Thoracic	M	12.01	166	7.71	136	156
	F	7.23		5.66		128
Lumbar	M	10.99	150	8.31	132	132
	F	7.31		6.30		116

It is evident that, despite the similar ages, overall relative weight gain of total carcass bone was greater in the present study than in Fourie's case. This difference is more marked between the males than the females, which may either be a breed characteristic or brought about by differential environmental effects. Secondly, it emerges that, with respect to differential vertebral growth, the ewes from the two sources are not markedly dissimilar, and that the major discrepancy is caused by the grossly enhanced masculine development of the cervical and thoracic vertebrae in the Icelandic, compared with the New-Zealand rams. Furthermore, this outstanding difference would appear to be associated with the even greater sex effect seen in the development of the skull of the Icelandic sheep, which largely reflects the greater extent of horn growth in the rams than in the ewes. Thus,

it is suggested that the comparatively enlarged anterior vertebral column in the Icelandic rams bears a direct relation to the excessive weight of the head of these animals. Such a functional relationship, between head weight and the growth of the thoracic spinal processes, was postulated by Hammond (1932) and should apply equally to the cervicals, as the weight of the head seeks support in attachments to both of these vertebral units.

To the author's knowledge, the gradients described among the cervical and thoracic vertebrae, have not previously been demonstrated in livestock. Again, it may be attempted to explain these in terms of post-natal changes in functional demand. Thus, the greatest degree of cervical differentiation occurred in the later growth phase and coincided with the highest relative rate of skull growth. The cervical pattern was such that the seventh vertebra, which has the weakest attachments with the ligamentum nuchae, supporting the head, also showed the least active growth, there being a posterio-anterior gradient of increasing relative growth rate. Moreover, the fastest growing thoracic vertebrae were those with the longest spinal processes, with which the ligamentum nuchae forms its attachments. One may therefore speculate, as if the observed differential patterns, being more marked in the males than in the females, represent an adaptation to the increasing burden of supporting the head, particularly in the rams as they approach maturity.

Fourie (1965) provided evidence for a growth gradient among the ribs; however, not as clear as we have demonstrated. The steepest rise in relative growth in the present data was seen from the ninth rib backwards, for which area Fourie (1965) did not present any values. It would seem likely that this development of the rib cage is a direct response to the growing pressure from the anterior alimentary tract, which, as has been shown (Chapter 4.), increases in weight after birth at a much higher rate than the thoracic organs.

With respect to dimensional growth, the general developmental patterns were not markedly dissimilar from previous findings. However, within the limbs, the changes in form of some individual bones, as well as those in the length ratios of different bones, deviated somewhat from the order described by Hammond (1932) and Pálsson and Vergès (1952), while being closer to Fourie's (1965) findings. This may be only natural, as the comparison of the different studies is confounded by the stage of maturity as well as by sex.

b) Genotype effects.

In evaluating the substantial difference in bone weight distribution, found between the three Edinburgh cannon lines, we face the same problem as before in not knowing the ultimate adult weight of the whole skeleton, or more importantly, the relative line difference at maturity. Nevertheless, it can be confidently concluded that the differences observed are in the main true selectional effects, not confounded by line differences in relative maturity. If they were not, the S-line should have a markedly heavier pelvis than the L-line, at constant total bone weight, and similarly, the proportional differences in the weight of the ribs would be greater than observed. Further to substantiate the conclusion, is the fact that the early developing limb bones constituted similar or higher proportions of the whole in the L-line at 2.0 kg carcass bone weight than in the S-line at 0.8 kg. Such a vast relative difference in skeletal weight at maturity can hardly be anticipated.

It is most interesting, in light of the different selection procedures applied, to compare the results from the two trials. Thus, in Edinburgh, the exercise, based on a single selection criterion, cannon bone length, has not only affected total skeletal weight, but simultaneously distorted skeletal proportions by exerting the greatest effects on the limb bones and most so on the bone selected for; whereas in Iceland, the more general approach, aiming at lighter bones and improved 'meatiness', has achieved a vast reduction in skeletal weight with only minimal effects on skeletal proportions. The major exception to the uniformity in the latter case, is seen in the head bones which have not been reduced in weight to the same extent as the rest of the skeleton, thus suggesting a greater resistance of these bones to genetic modification, as has been found with respect to nutritional effects (Elsley, McDonald and Fowler, 1964).

The important lessons to be learned, are: (1) that bone weight distribution is not an inflexible characteristic, but can be modified by systematic genetic selection; (2) therefore, the selection criteria in all breeding work must be carefully chosen to meet the objectives, for instance, whether one seeks to change skeletal weight in general, or to do so in a differential fashion. (3) Using the weight of a single bone, e.g. the cannon bone, to predict the weight of the whole

skeleton may be unsafe over a range of genotypes, unless these are separately accounted for. This was acknowledged by Pålsson (1940); however, in most practical circumstances, the bias is not likely to be of major significance, unless extreme genotypes are involved.

It is evident that the changes brought about in the weight of the limb bones in the Edinburgh cannon lines, have been achieved largely by altering their length, as the thickness of the same bones was either unaffected or inversely related to the changes in length. The same trend is shown in the Icelandic data, in as much as the type differences were greater in length than in thickness, this being most marked for the cannon bones. Thus, the S-line/type show the skeletal form postulated by Hammond (1932) and Pålsson (1940) to be indicative of early maturity, and this we have also observed. Pålsson (1971) further postulated the shape of the fore cannon bone to be strongly associated with the relative amounts of muscle and bone in the carcass. As an index of shape, he used the ratio of smallest circumference/ weight of the cannon bone and found this to be positively correlated with the muscle: bone ratio. While not having statistically analysed the relationship between these ratios in the present data, the mean values, at comparable stages of development, are presented in table 7.3.2.

Table 7.3.2. Effect of cannon line/conformation type on muscle: bone ratio and shape of the fore cannon bone.

Source	Line/ type	Muscle: bone ratio	Fore cannon bone C/Wt. (mm/g)
Edinburgh	L	4.36	1.12
	S	4.52	1.44
Iceland	L	4.74	1.21
	S	5.56	1.46

It has already been explained (Chapter 5.) that, with respect to the muscle: bone ratio, the two sets of results are not directly comparable, due to greater moisture loss after slaughter in Edinburgh material. Bearing that in mind, the within breed differences in the two ratios, support Pålsson's (1971) hypothesis; however, the dispro-

portionate effects in the two data sets would suggest that an effective selection for improving the muscle: bone ratio should include other criteria as well as cannon bone shape. In this respect, valuable information was provided by the work of Kempster (1978), with cattle, and Kempster et al. (1981), with sheep. While in both studies finding the muscle: bone ratio to be positively associated with conformation score, the strength of that relationship was insufficient to explain the differences observed between certain breeds, such as in the Suffolk and the Texel. Kempster (1978) suggested that breed difference in bone density might offer a clue towards solving the question.

Probably the most surprising discovery, regarding the skeleton, was that of the highly significant line effect on the number of lumbar vertebrae in the Edinburgh sheep. Variation in vertebral number is by no means uncommon among domesticated animals and has been reported in sheep for all sections of the spinal column (Pålsson, 1940; Fourie, 1965); though, in general, the number of cervical vertebrae is considered to be most constant. It is generally acknowledged that the number of the different vertebrae is an inherited characteristic (Fourie, 1965), and Pålsson (1940) concluded that the provision of effective means, by which the animal breeder could increase the number of thoracic and, in particular, lumbar vertebrae, would be a significant step towards improving the body proportions of meat producing animals. While no biological explanation can be offered, it is clear that the singular selection for a short cannon bone has produced a remarkable increase in the incidence of seven lumbar vertebrae, and vice versa, which undoubtably has contributed to the observed line differences in carcass form, joint proportions and muscle weight distribution.

c) Sex effects.

The major sex differences in skeletal weight proportions at 20-24 weeks represent the increasing masculine superiority in the development of the skull and the anterior spinal column. The inhibited growth of these late maturing parts, in the females is the cause for the higher proportions of the earlier developing mandible and long limb bones in that sex at 74 weeks, which is in accordance with earlier findings (Pålsson, 1955; Fourie, 1965). However, it is not entirely accurate to describe these differences solely in terms of the

males having attained a more advanced state of development as Pålsson (1955) did. Thus, the late developing pelvis, as well as the sacrum, still constituted higher proportions of the whole in the females, while the scapula and the ribs were not markedly dissimilar in the two sexes. Simply to represent differences in relative maturity, the pelvis, scapula, sternum and ribs should be better developed in the oldest rams, compared with the ewes, no less than the cervical and thoracic vertebrae. One must therefore conclude that the observed effects are of a fundamental nature, the different patterns having evolved in response to functional necessity. Further in support of that is the relatively wider shape of the pelvis and the sacrum in the females which is an obvious advantage in relation to their function to give birth to the young. Similarly, the enhanced thickness growth of the long bones in the rams, compared with the ewes, also found by Hammond (1932), Pålsson and Vergés (1952) and Fourie (1965), could be a consequence of the greater load supported by these bones in the masculine sex.

PLATE 7.1. DEVELOPMENTAL CHANGES IN SKELETAL PROPORTIONS (ICELAND).

A: FORE LIMB (from left to right: metacarpus (cannon bone), radius-ulna, humerus, scapula).

Note the relative changes in length of the different bones, from birth to 74 weeks of age; also the change in shape of the humerus and the scapula and the relatively greater thickness of these bones in the S-type, compared with the L-type.

PLATE 7.1. (Continued)

B: HIND LIMB (from left to right: metatarsus (cannon bone), tibia-fibula, femur, pelvis).

Note the similar relative changes in length as in A; also the marked change in shape of the pelvis and the different length relationships between the pelvis and the femur in the two types at 74 weeks of age.

PLATE 7.1. (Continued)

C: 7th RIB / METACARPUS.

The rib increases in length ca. 1.5 times more than the metacarpus; its spring also increases relatively more than its length. Note, further, the greater spring of the ribs in the S-type and the somewhat different length relationships between the two bones at birth, indicating a more advanced development of the S-type, compared with the L-type.

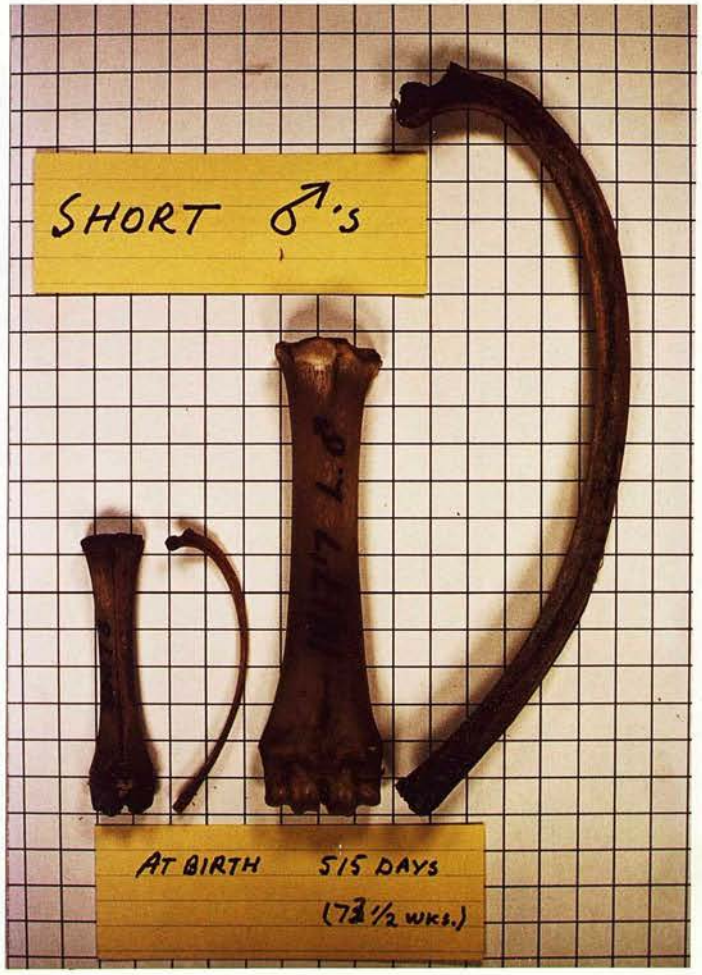
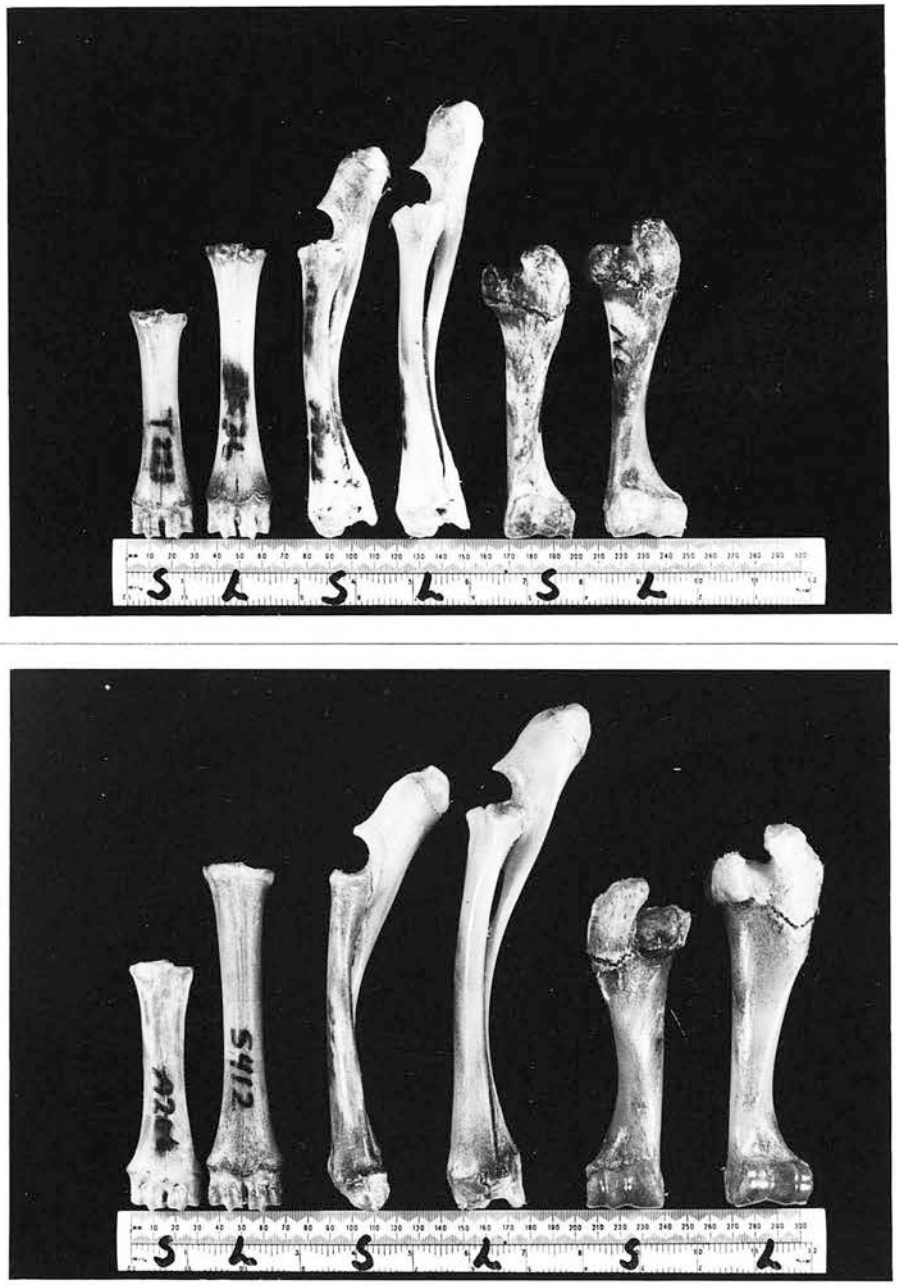


PLATE 7.2. EFFECT OF CANNON LINE ON SKELETAL PROPORTIONS (EDINB.)

(I) Pair of S- (left) and L- (right) lambs, representing mean dimensions for each line (see table 7.2.6.).

(II) Pair of S- and L-lambs from maturity group.



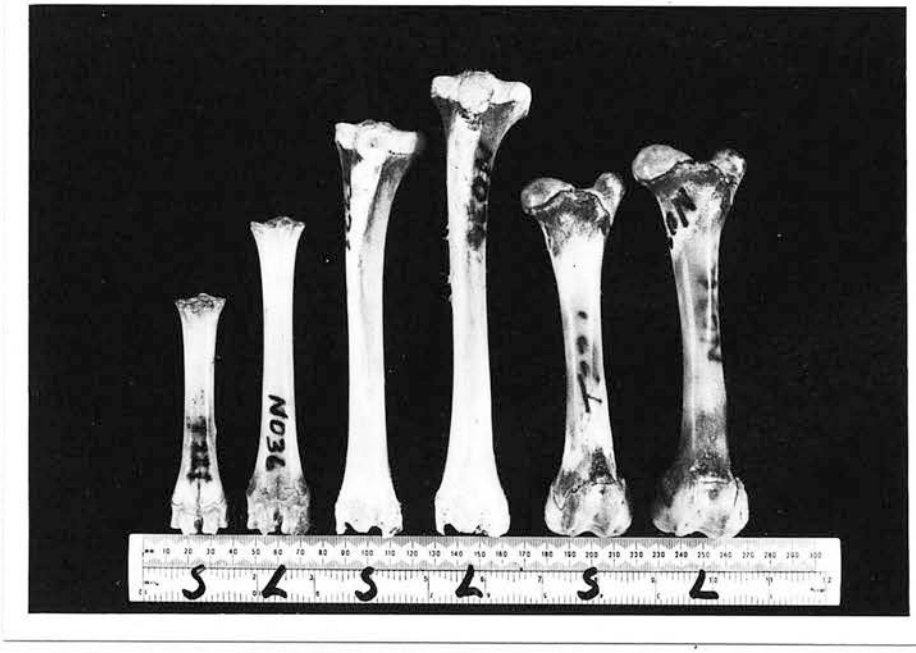
(I)

(II)

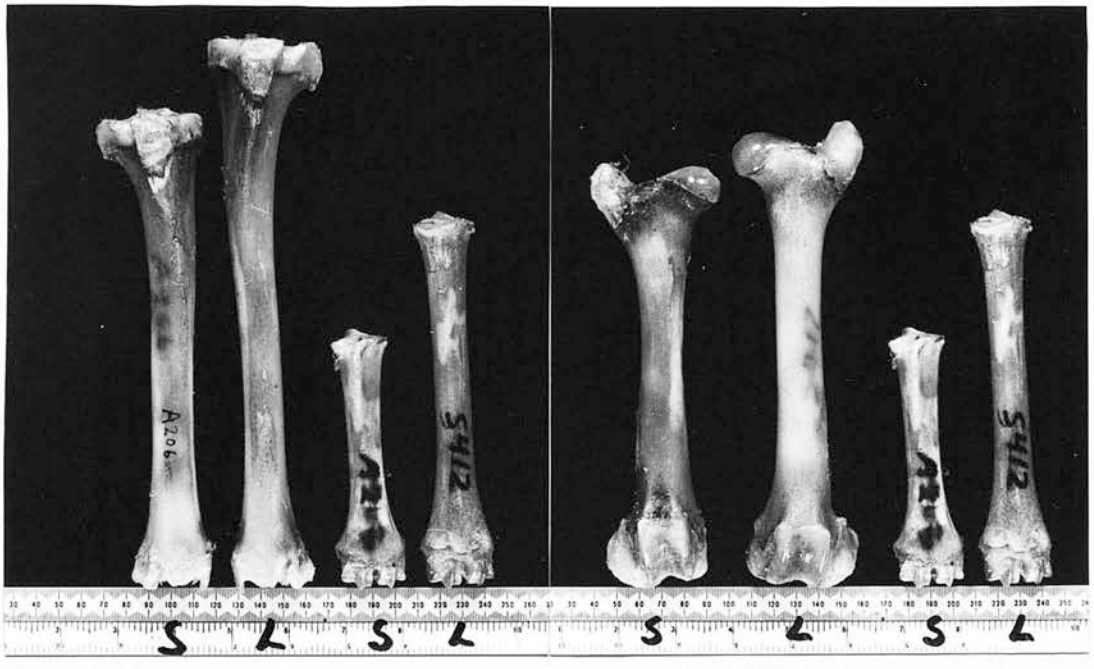
A: LONG BONES OF FORE LIMB.

The relative line difference is greatest in the length of the metacarpus and smallest in the humerus. Note also the different shape of the metacarpal bones.

PLATE 7.2. (Continued)



(I)



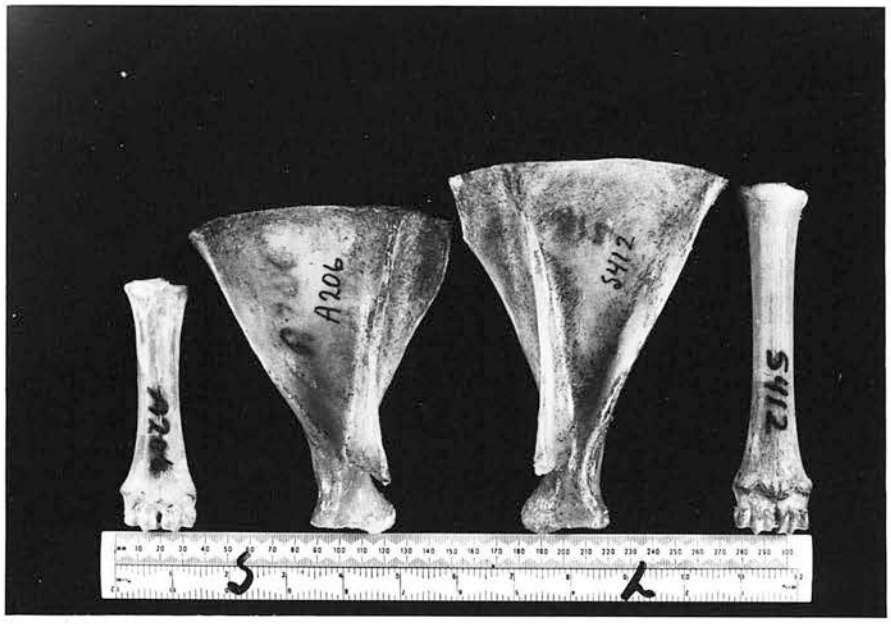
(II)

B: LONG BONES OF HIND LIMB.

Note the same pattern as in A, the difference in length between the two lines gradually declinining from the metatarsus to the femur.

PLATE 7.2. (Continued)

(I)

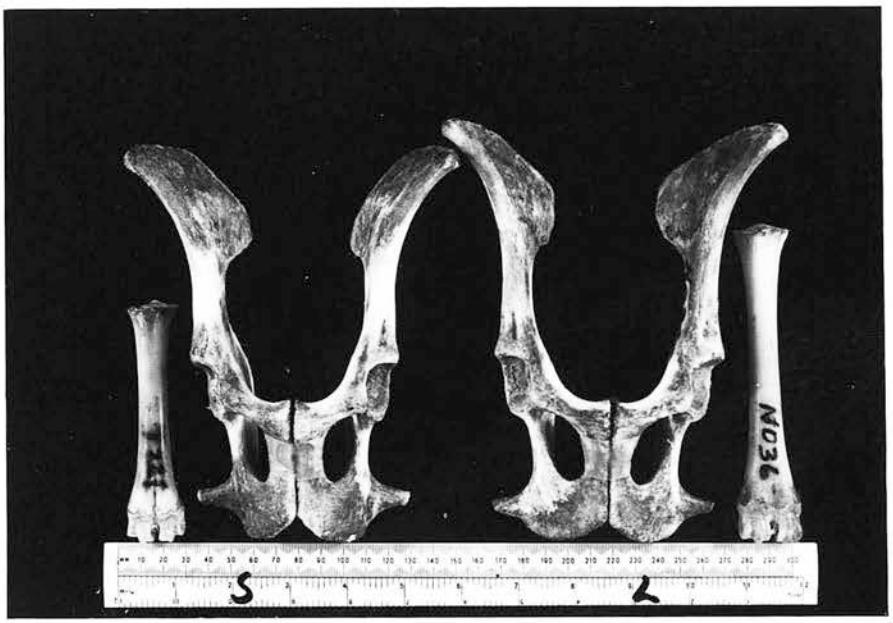


(II)

C: SCAPULA / METACARPUS.

Note, that in the L-line, the metacarpus is almost as long as the scapula, whereas in the S-line, the difference is considerable. Note also the different shape of the scapula, this being relatively broader in the S-line.

PLATE 7.2. (Continued)



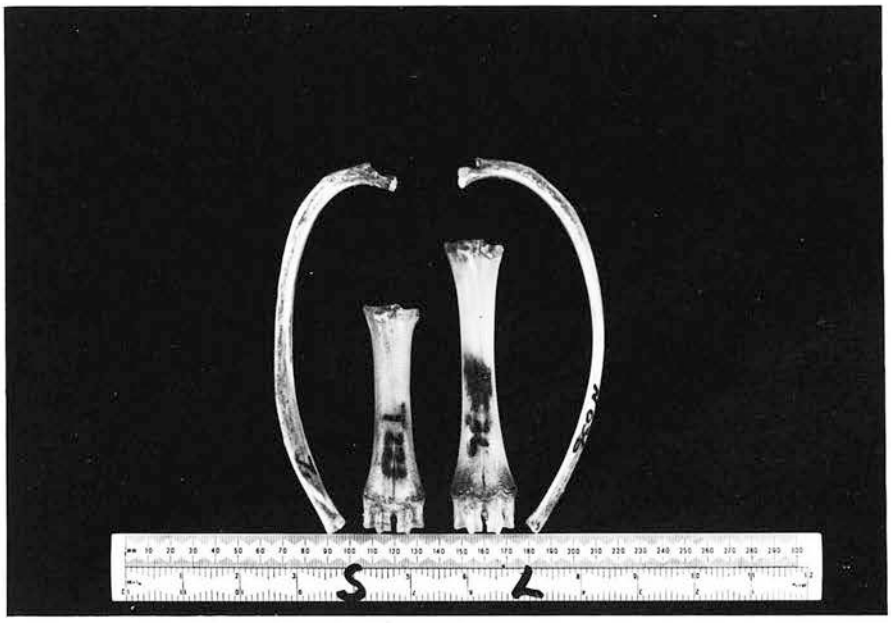
(I)

(II)

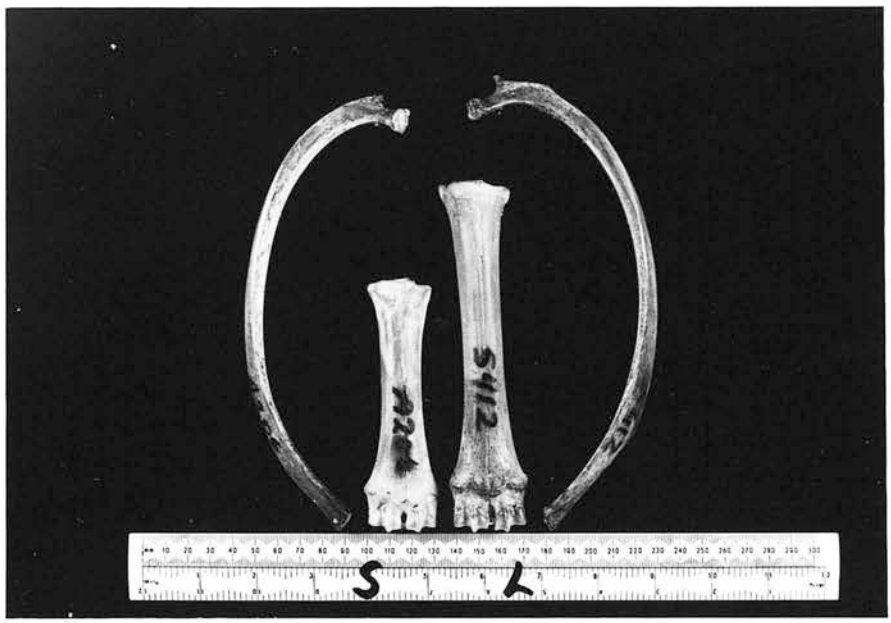
D: PELVIS / METATARSUS.

The pelvis is longer, relative to the metatarsus, in the S-line; its shape is also different, the L-line tending to have a longer and relatively narrower pelvis than the S-line.

PLATE 7.2. (Conitnued)



(I)



(II)

E: 7th RIB / METACARPUS.

Despite a large difference, between the L- and S-lines, in the length of the metacarpus, there is virtually no difference in the length of the rib. This concludes the series of pictures, illustrating, how the selection effects have been strongest at the extremities, while diminishing stepwise towards the latest maturing trunk bones.

PLATE 7.3. EFFECT OF CONFORMATION TYPE ON SKELETAL PROPORTIONS (ICELAND).

(Pair of equally heavy males from the 48 weeks slaughter group. The relative differences are representative of the average.)

A: LONG BONES OF THE LIMBS.

The relative type difference in length of the metacarpal / tarsal bones tends to be marginally greater than in that of the other long bones. However, in comparison to the Edinburgh selection (PLATE 7.2.A&B), the differential effect on these bones in the Icelandic sheep is only minimal.

PLATE 7.3. (Continued)

B: SCAPULA, 7th RIB AND PELVIS.

Note the greater spring, relative to length, of the S-type rib and the wider shape of the S-type pelvis, particularly at the tuber ischii.

CHAPTER 8.

THE DEVELOPMENT OF CARCASS FAT DISTRIBUTION

8.1. INTRODUCTION.

Hammond (1932) and Pålsson and Vergès (1952), with sheep, demonstrated similar growth gradients within each of the carcass fat depots to those found within the whole carcass and its other major component tissues. Apart from the brief mention of the subject by Seebeck (1968a), little attention appears to have been paid, in sheep, to the development of fat weight distribution between the various carcass regions.

There are, however, sound reasons for studying this aspect of development. (1) In general, uniform distribution of both subcutaneous and intermuscular fat is desirable as 'patchy fat' may necessitate excessive trimming of some joints. Further, an even layer of subcutaneous fat will ensure a better protection for the underlying tissue, which is most important in circumstances, where meat is frozen. (2) Single measurements of fat thickness are frequently used to estimate total carcass fat. The validity of such estimates must depend on the constancy of fat weight distribution, as well as on the partition between the subcutaneous (SF) and intermuscular (IF) fat depots.

The developmental patterns of fat deposition in different carcass regions have recently been studied in cattle by Seebeck and Tulloh (1968), Kempster, Avis and Smith (1976a) and Berg, Andersen and Liboriussen (1978c), and in pigs by Richmond and Berg (1971b), Davies and Pryor (1977) and Kempster and Evans (1979). Detailed comparison of the various results is complicated by varying jointing techniques and the lack of clear physical, anatomical boundaries between the different sites of fat depostion. However, the three cattle studies show general agreement in suggesting a low growth intensity in the distal limbs, with gradients of increasing relative growth rate going up the limbs, meeting in the rib or loin regions and reaching a climax in the flank regions. While, in general, both the SF and IF depots were observed to follow similar patterns, Seebeck and Tulloh (1968) and Kempster *et al.* (1976a) found the growth coefficient for IF in the thin flank to be markedly higher than that for SF. The results of Kempster and Evans (1979), in the pig, are generally consistent with those obtained from cattle. However, the fastest relative growth was observed in the back region, rather than more ventrally on the sides. Davies and Pryor (1977) determined

growth gradients for intramuscular fat of muscle groups in the pig, relative to total intramuscular fat, and found those to reflect the developmental patterns of the entire muscles.

Breed differences in fat weight distribution between carcass joints have been reported in sheep by Seebeck (1968a), in cattle by Harte and Conniffe (1967), Seebeck (1973 b), Kempster et al.(1976 a) and Berg et al. (1978 c), and in pigs by Richmond and Berg (1971 b) and Kempster and Evans (1979). In general, these effects have been regarded as relatively small and commercially unimportant. However, Seebeck (1968 a) found the pure Merino to contain 38% more IF in the neck, 9% less in the thorax and 11% more in the loin + flank than its cross with the Border Leicester x Dorset Horn. Similarly, while greater differences in SF were observed within the thorax and loin + flank, the neck proportions did not differ significantly. Likewise Kempster et al.(1976 a), comparing 15 different cattle breeds and crosses, found differences in the fat contents of the various joints amounting to 30% between the most extreme breed types. While considering these differences small, the authors made the point, that the variation in SF distribution was likely to be of a greater magnitude at levels of fatness above those in their study.

There is little published information on the influence of sex on fat weight distribution. Seebeck (1968 a) found no sex differences in sheep with respect to SF, while the ewes had 15% more IF in the loin + flank than the rams, a difference that could reflect on the stage of maturity. In the pig, Richmond and Berg (1971 b) found barrows to contain a higher percentage of their IF in the hind-quarter and less in the fore-quarter than gilts, while no such differences were found in the SF depot. In contrast, Kempster and Evans (1979) found somewhat larger differences between barrows and gilts with respect to SF than IF; most of which, however, were small and unsystematic with regard to developmental order.

On account of the scarce documentation, no general conclusion can be drawn; there is, however, at present, a greater evidence for genetic than sexual effects on fat weight distribution over the different carcass regions.

8.2. RESULTS

a) Common developmental patterns.

It is apparent from the two sets of growth coefficients in tables 8.2.1. and 8.2.2. that, in general, the developmental patterns were similar for both the subcutaneous and intermuscular fat depots. Growth intensity was lowest in the shank, followed by the neck and gigot joints, while reaching a maximum in the rib and loin regions. It should be remembered that the secondary shoulder joint in Iceland included the neck and shank as well as the breast. Further, it is worth noting that the coefficients were determined over different age intervals in each trial.

Quadratic trends indicated a rise in relative growth rate in the secondary shoulder joint, particularly for SF in the neck, with increasing level of fatness. Simultaneously, growth coefficients were declining for SF in the prime rib and for IF in the whole rib joint in the Edinburgh sheep. In Iceland, SF reached a peak intensity of growth in the dorsal area of the rib and loin in early life, which subsequently evened out, whereas in Edinburgh the fastest rate of SF deposition was attained in the loin flank at a later stage of growth.

As regards IF, the Edinburgh results show the fastest relative growth in the rib joint, while in Iceland, the loin flank was the area of most active deposition. Judging from quadratic trends in the log-log regressions, IF showed a greater constancy in relative growth rates, within the different joints, over the ranges studied.

b) Genotype effects on fat weight distribution.

With respect to relative growth coefficients, there were no significant differences between the three Edinburgh cannon bone lines. Similarly, in Iceland, such effects were non-significant for SF, whereas for IF significant type differences were observed in two joints. Thus, in the secondary rib, the growth coefficients for IF were 1.29 and 1.17 ($p < 0.05$), and in the prime loin 1.20 and 1.08 ($p < 0.05$), for the L- and S-types, respectively.

The percentage distribution of SF and IF over the carcass, for the different genotypes, is shown in tables 8.2.3. and 8.2.4. for the Edinburgh and Icelandic trials, respectively. Where adjusted to equal total depot weight, the means for the covariates were chosen as to

Table 8.2.1. Relative growth coefficients (b) relating the weight of fat in joints to that of the total depots+. (Edinburgh).

Joint	Overall b	SE	Total = 1.0 kg b	Total = 3.0 kg b	Signific. of diff.
A: Subcutaneous fat.					
Shoulder + breast	0.92	0.035	1.02	0.83	*
Neck	0.88	0.109	0.67	1.07	*
Shank	0.62	0.100			
Rib	1.13	0.027			
Prime loin	1.11	0.045			
Loin flank	1.14	0.062	0.95	1.31	*
Gigot	0.93	0.031			
B: Intermuscular fat.					
Shoulder + breast	0.97	0.032			
Neck	0.99	0.124			
Shank	0.53	0.187			
Rib	1.20	0.060	1.44	1.01	*
Prime loin	1.10	0.086			
Loin flank	0.91	0.149			
Gigot	0.91	0.058			

+) Estimated with 98 lambs on the feeding trial and adjusted to constant daily D.M. intake.

Table 8.2.2. Relative growth coefficients (b) relating the weight of fat in joints to that of the total depot[+]. (Iceland).

Joint	Overall		Total = 0.5 kg	Total = 2.0 kg	Signific. of diff.
	b	SE	b	b	
A: Subcutaneous fat.					
Prime shoulder	1.03	0.033			
Sec. shoulder	0.86	0.024	0.79	0.96	*
Prime rib	1.20	0.031	1.30	0.91	***
Sec. rib	1.16	0.023			
Prime loin	1.20	0.028	1.25	1.03	*
Loin flank	1.00	0.037			
Prime gigot	0.95	0.018			
Gigot flank	0.89	0.029			
B: Intermuscular fat.					
Prime shoulder	1.00	0.019			
Sec. shoulder	0.93	0.033	0.71	1.00	**
Prime rib	1.16	0.036			
Sec. rib	1.23	0.038			
Prime loin	1.14	0.029			
Loin flank	1.36	0.038			
Prime gigot	0.79	0.019			
Gigot flank	1.03	0.032	1.26	0.92	**

+) Estimated with 56 lambs (6 - 24 weeks) and adjusted for conformation type and sex.

Table 8.2.3. Effect of cannon line on fat weight distribution in the carcass+. (Edinburgh).

Fat in:	Line	SF (Total = 2.4 kg)				IF (Total = 3.0 kg)			
		Wt. (g)		% of	Relat. diff.	Wt. (g)		% of	Relat. diff.
		Mean	SE	tot.SF	(C=100)	Mean	SE	tot.IF	(C=100)
Shoulder	L	645	11.0	26.9	99	1422	13.6	47.4	102
	C	651	10.6	27.1		1393	12.6	46.4	
	S	660	13.2	27.5	101	1400	16.6	46.7	101
Rib	L	479	7.8	20.0	102	584	11.2	19.5	99
	C	470	7.2	19.6		588	10.4	19.6	
	S	465	9.4	19.4	99	581	13.4	19.4	99
Loin	L	454[a]	6.5	18.9	93	355[a]	5.9	11.8	92
	C	486[b]	6.5	20.3		387[b]	6.0	12.9	
	S	494[b]	8.6	20.6	102	396[b]	8.1	13.2	102
Gigot	L	804	14.4	33.5	104	623	11.6	20.8	100
	C	774	13.2	32.3		624	11.0	20.8	
	S	771	17.2	32.1	100	615	14.2	20.5	99

+) Estimated by regressions (98 lambs on feeding trial) and adjusted to constant daily D.M. intake.

Table 8.2.4. Effect of conformation type on fat weight distribution in the carcass[+]. (Iceland).

A: Subcutaneous fat.

SF in:	Type	Total SF = 2.0 kg[x]				Age: 74 wks.[xx]		
		Wt. (g)		% of	Relat. diff.	% of tot. SF		Relat. diff.
		Mean	SE	tot. SF	(S=100)	Mean	SE	(S=100)
Prime shoulder	L	223 *	10.6	11.2	114	12.3 *	0.81	130
	S	196	7.6	9.8		9.4	-	
Secondary shoulder	L	354 N.S.	15.0	17.7	106	17.3 *	0.44	113
	S	333	9.0	16.7		15.3	-	
Prime rib	L	179 N.S.	9.2	9.0	89	10.4 N.S.	0.70	85
	S	201	6.6	10.1		10.7	-	
Secondary rib	L	241 N.S.	7.8	12.1	100	11.6 N.S.	0.72	83
	S	242	6.4	12.1		13.9	-	
Prime loin	L	221 *	11.4	11.1	85	14.3 N.S.	0.62	97
	S	260	8.6	13.0		14.7	-	
Loin flank	L	130 N.S.	6.8	6.5	92	6.2 N.S.	0.44	97
	S	142	6.2	7.1		6.4	-	
Prime gigot	L	476 N.S.	12.0	23.8	98	21.2 N.S.	0.91	93
	S	487	10.0	24.4		22.8	-	
Gigot flank	L	139 N.S.	5.6	6.9	107	6.7 N.S.	0.44	126
	S	130	4.4	6.5		5.3	-	

x) Estimated by regressions.

xx) Means of percentages for individuals.

Total SF wt. - L = 3144g
S = 4741- (SE = 503.0, $p < 0.10$).

Table 8.2.4. (continued)

B: Intermuscular fat.

IF in:	Type	Total IF = 2.5 kg [x]					Age: 74 wks. [xx]			
		Wt. (g)			% of tot.SF	Relat. diff. (S=100)	% of tot. IF			Relat. diff. (S=100)
		Mean		SE			Mean		SE	
Prime shoulder	L	603	N.S.	9.2	24.1	96	27.1	N.S.	0.90	104
	S	630		8.8	25.2		26.1		-	
Secondary shoulder	L	503	**	13.5	20.1	110	19.9	N.S.	0.98	100
	S	463		12.4	18.5		19.9		-	
Prime rib	L	228	N.S.	6.3	9.1	95	9.5	N.S.	0.39	91
	S	240		6.3	9.6		10.5		-	
Secondary rib	L	260	N.S.	5.4	10.4	97	10.6	N.S.	0.68	87
	S	268		5.2	10.7		12.2		-	
Prime loin	L	203	N.S.	4.5	8.1	95	7.3	N.S.	0.45	92
	S	213		4.5	8.5		7.9		-	
Loin flank	L	95	***	2.7	3.8	86	4.2	N.S.	0.27	82
	S	110		2.9	4.4		5.1		-	
Prime gigot	L	410	***	6.5	16.4	108	14.7	*	0.52	114
	S	380		5.4	15.2		12.8		-	
Gigot flank	L	190	N.S.	5.2	7.6	105	6.7	*	0.35	122
	S	183		5.2	7.3		5.5		-	

x) Estimated by regressions.

xx) Means of percentages for individuals.

Total IF wt. L = 4384 g
S = 5560 - (SE = 448.6, $p < 0.10$)

show the distribution of each depot at a similar degree of carcass development, or on average at approximately 16 kg carcass weight.

In Edinburgh, the cannon bone line effects were only marginal except in the loin joint within which the S-line contained 9% ($p < 0.05$) and 11% ($p < 0.01$) more of its SF and IF, respectively, than did the L-line.

In Iceland, the differences were more widespread and generally greater at 74 weeks than at the earlier comparisons, when total depot weights were held constant. The two depots were differentially affected by the type of comformation. Thus, at constant depot weight, the L-type had the greatest excess over the S-type in SF in the prime shoulder (14%, $p < 0.05$), while the corresponding differences in IF were seen in the secondary shoulder (10%, $p < 0.01$) and the gigot (8%, $p < 0.001$). In contrast, the differences in favour of the S-type, were largest in the prime rib (12%, $p < 0.05$) and prime loin (17%, $p < 0.01$) joints, regarding the SF; the excess in proportion of IF being greatest in the loin flank (16%, $p < 0.01$). In particular, it is worth drawing attention to the differential effect on the two depots in the prime gigot joint (table 8.2.4.).

c) Effects of sex on fat weight distribution.

Relative growth coefficients for SF in the various joints did not differ significantly between the two sexes; however, there was a tendency for higher relative growth rates in the dorsal joints of males and ventral joints of females. For IF, the males had significantly higher growth coefficients in the secondary rib and prime loin joints, or 1.29 and 1.20, compared with 1.17 and 1.08 ($p < 0.05$) in the females, respectively.

Like before, with the other tissues, comparisons of percentage distribution have been made at equal ages, rather than at equal total depot weight (table 8.2.5.), from which several interesting features emerge. Firstly, the influence of sex was enhanced with increasing age. Secondly, the two depots were not alike in the nature or magnitude of sexual characteristics. Males had the greatest advantage in the development of both SF and IF in the secondary shoulder, or 30% ($p < 0.001$) and 21% ($p < 0.05$) at 74 weeks, respectively; in which respect the superior masculine development of the neck was an important contributing factor. The proportion of both SF and IF in the

Table 8.2.5. Effect of sex on fat weight and distribution[x]. (Iceland).

A: Subcutaneous fat.

SF in joint	Sex	Age: 20 - 24 wks.			Age: 74 wks.		
		% of tot.SF		Relat. diff. (F=100)	% of tot.SF		Relat. diff. (F=100)
		Mean	SE		Mean	SE	
Total SF (wt. in g)	M	1819 N.S.	76.9	95	4038 N.S.	503.0	105
	F	1924	-		3847	-	
Prime shoulder	M	10.8 N.S.	0.57	111	10.9 N.S.	0.81	101
	F	9.7	-		10.8	-	
Sec. shoulder	M	18.0 N.S.	0.66	99	18.4 ***	0.44	130
	F	18.2	-		14.2	-	
Prime rib	M	9.3 N.S.	0.34	93	10.7 N.S.	0.70	89
	F	10.1	-		12.0	-	
Sec. rib	M	11.6 *	0.39	91	11.4 *	0.71	81
	F	12.8	-		14.1	-	
Prime loin	M	11.3 N.S.	0.39	95	14.0 N.S.	0.62	93
	F	12.0	-		15.0	-	
Loin flank	M	7.1 N.S.	0.26	107	6.8 N.S.	0.44	119
	F	6.7	-		5.7	-	
Prime gigot	M	24.9 N.S.	0.50	104	21.6 N.S.	0.91	97
	F	24.0	-		22.4	-	
Gigot flank	M	6.9 N.S.	0.25	105	6.2 N.S.	0.44	107
	F	6.6	-		5.8	-	

CONTD.

Table 8.2.5. (continued).

B: Intermuscular fat.

IF in joint	Sex	Age: 20 - 24 wks.			Age: 74 wks.		
		% of tot. IF		Relat. diff. (F=100)	% of tot. IF		Relat. diff. (F=100)
		Mean	SE		Mean	SE	
Total IF (wt. in g)	M	2640 N.S.	75.1	99	5493 N.S.	448.6	123
	F	2669	-		4452	-	
Prime shoulder	M	25.1 N.S.	0.52	102	26.6 N.S.	0.90	100
	F	24.5	-		26.6	-	
Sec. shoulder	M	20.5 **	0.44	109	21.8 *	0.98	121
	F	18.8	-		18.0	-	
Prime rib	M	9.5 N.S.	0.26	102	10.7 +	0.39	114
	F	9.3	-		9.3	-	
Sec. rib	M	10.4 N.S.	0.35	94	11.0 N.S.	0.68	94
	F	11.1	-		11.8	-	
Prime loin	M	7.8 *	0.23	91	6.9 +	0.45	82
	F	8.5	-		8.4	-	
Loin flank	M	4.0 *	0.16	89	3.9 *	0.27	73
	F	4.5	-		5.4	-	
Prime gigot	M	14.7 N.S.	0.39	98	12.9 +	0.52	88
	F	15.4	-		14.6	-	
Gigot flank	M	7.4 N.S.	0.24	98	6.2 N.S.	0.35	105
	F	7.5	-		5.9	-	

+) $0.05 < p < 0.10$.

x) Adjusted for conformation type and type of birth.

prime shoulder was remarkably similar in the two sexes. The greatest female excess over males was observed with SF in the secondary rib (10-24, $p < 0.05$) and with IF in the loin flank (11-21%, $p < 0.05$). Both depots also showed a higher degree of development in the prime loin of the females, the difference, however, only being significant for the IF. In contrast, the males showed a tendency to deposit more of their SF in the loin flank. Differential effects were also observed in the prime gigot, within which the proportion of SF was not significantly different between the sexes, whereas the females at 74 weeks had an advantage of 13% ($p < 0.10$) in the proportion of IF in this joint.

8.3. DISCUSSION

a) Common developmental patterns.

Like previously cited workers using sheep, cattle and pigs, the commonly acknowledged centripetal growth gradients were found to be at work within each of the two carcass fat depots, no less than within the other carcass tissues. Thus, the information available at present is consistent for these three species of livestock, in showing increasing growth intensity from the distal limbs and neck into the central region of the trunk. What is not as clear yet, is the exact location of termination of the centripetal growth waves; nor is it clear if this is the same for both the depots. The two experiments are in conflict in this respect. The Icelandic data showed the relative growth of SF to reach a climax and terminate in the lumbar region, i.e. the prime loin joint, whereas the most active centre for IF deposition was found to be the loin flank. Not only is this indicated by the growth coefficients over the 6-24 weeks age interval, but also by the changes in percentage distribution of fat from 6 weeks to 74 weeks of age (table 8.3.1.), which clearly show the greatest relative increase of SF in the prime loin and of IF in the loin flank.

Evidence for a similar effect in cattle can be seen in the results of Seebeck and Tulloh (1968), though Kempster *et al.* (1976 a) found the highest relative growth coefficients for both the depots to be in the thin flank.

The opposite trend in the Edinburgh data forbids a general conclusion to be drawn. There is a reason to believe, however, that this may have been influenced by the different jointing technique. The

Table 8.3.1. Changes in percentage distribution of fat with age. (Iceland).

Joint	SF in joint-% of total SF		IF in joint-% of total IF	
	6 wks.	74 wks.	6 wks.	74 wks.
Prime rib	7.3	11.4	7.1	10.0
Sec. rib	9.0	12.8	8.0	11.4
Prime loin	8.8	14.5	6.6	7.6
Loin flank	6.1	6.3	2.4	4.6

'Edinburgh-flank' was a smaller joint than its counterpart in the Icelandic work. That per se may be of significance. Secondly, the standards for marking the 'de-flanking line' in Edinburgh were more prone to erroneous variation, due to frequent irregularities in the length of the 13th rib, on which the separation of flank from prime loin was based. Thirdly, the inevitable errors associated with the cutting of the flank would be the more serious in the Edinburgh dissection, since the flank was smaller. It can be seen, not only for the fat, but for any estimates of means or coefficients relating to the 'Edinburgh-flank', that the standard errors are relatively high. The reason is likely to be one of experimental error rather than of natural variation; thus the corresponding results must be interpreted with caution.

b) Genotype and sex effects.

As long as the full potential of the different genotypes for fat deposition is unknown, it seems most logical to compare the distribution of SF and IF at equal total depot weight, respectively. Three other alternatives were tested, i.e. at equal age, at equal carcass weight and at equal level of percentage carcass fatness, all of which yielded a similar picture for genotype effects, although the degree of differences varied somewhat according to the covariate chosen. Conversely, it is considered more appropriate to compare the two sexes at equal ages, due to the large difference that is known to exist in mature weight, while again, we do not know the full potential of either sex for fat deposition.

The genotype differences in each trial, in general, are indicative of earlier maturity in the short-legged sheep than in the leggier type.

However, this does not fully explain the effects observed, as the magnitude of line/type differences was not consistant with the order of relative growth coefficients for the various joints. With respect to sex, the differences between males and females can not be regarded as simply reflecting different maturity types. In fact, some of the differences were directly antagonistic to such an effect.

It was argued earlier that uniform fat weight distribution was a desirable carcass characteristics. As a measure of uniformity the variation in the ratio of fat to muscle, among the different carcass joints has been examined in the Icelandic data. The coefficients of variation indicated a somewhat greater uniformity in the S-type and the males, as compared with the L-type and the females, respectively. However, these differences were small and unlikely to be of any commercial significance.

CHAPTER 9.

DISCUSSION AND CONCLUSIONS

It is intended, in this section, to draw together and discuss some of the previously described findings, in an attempt to evaluate their theoretical or practical implication.

In the main, two methods have been applied to express differential body growth: the relative growth coefficients, derived from Huxley's (1932) allometric power function; and relative weight increases, i.e. the multiplication of weight of an organ or part from birth to varying ages. In addition, the changes in the ratios of one part to another, or to the whole, have been expressed for a number of components. Overall, the different methods have led to the same conclusions, regarding the developmental order of different body parts.

Tulloh (1963) discouraged the use of ratios or percentages in presenting growth data, on the grounds that these normally complicated what might otherwise be simple relationships. On the contrary, we consider simplicity to be the chief merit of these methods. While it is true that the mathematical implications, if pursued, may be unnecessarily complex, there is no clearer way of comprehending the developmental changes, than following the changes in part to part, part to whole or part to time relationships throughout the growing period. As far as the understanding of the 'normal' growth patterns is concerned, little additional information appears to be gained by applying the 'more sophisticated' regression equations. However, the regressional approach has certain important advantages over the simple ratios: (1) It has a predictive value within a discontinuous range of data; (2) the coefficients are easy to evaluate in statistical terms; and (3) it is less specific with respect to the experimental design and can be applied to data unsuitable for the other types of analysis, as for instance was the case with the present Edinburgh material.

In applying mathematical equations, such as Huxley's allometric formula, to growth data, one must be extremely careful not to take the allometric law for granted, unless convinced by thorough testing, as there are no intrinsic biological laws which make it apply exactly (Fowler, 1968). In the present study, at all anatomical levels, allometric constancy was the exception rather than the rule, when considering any extended periods of growth. Nevertheless, the equation could be usefully applied over restricted age intervals, the resulting coefficients then providing an approximation of the changing developmental

patterns. To what extent the fluctuations, observed in relative growth rates, are an inherent part of the normal growth process, as opposed to environmental influences, cannot be judged; these were only too clear to be ignored and must be taken account of in any detailed study of growth and development.

In accordance with earlier workers, the present study demonstrated a distinct order of development within the animal's body. Thus, the carcass grew marginally faster than the combined non-carcass components, while within the carcass per se the order of increasing growth intensity of its major tissues was bone, muscle, intermuscular fat and subcutaneous fat. Also within each of the tissues, there were consistent gradients of increasing intensity from the extremeties into the trunk, terminating in the thoracic-lumbar-abdominal area or the neck. It was particularly noteworthy in early life, how all the tissues, while as entities growing at vastly different relative rates, were virtually identical with respect to regional growth gradients. This raises a fundamental question in relation to the underlying basis of differential growth. Many authors, including Pålsson (1955) and Fowler (1968), have explained this phenomenon in terms of adaption by the body to meet with changes in functional requirements. However, Elsley, McDonald and Fowler (1964) and Fowler (1968) emphasized the distinct functional nature of fatty tissue, this being in the main an inert energy store and should not therefore in their opinion, be included in a standard for analysing growth data. In light of the highly regular pattern observed in the development of each of the carcass fat depots, this view would seem to be contradictory to the functional explanation of differential growth. Or, why does fat, if largely metabolically inert, as maintained by Fowler (1968), with no other apparent function, follow the same pattern of development as the structural tissues, muscle and bone, if the latter have adapted to this pattern as a consequence of functional necessity. It is certainly true that fat is a more variable product of growth than muscle or bone and undoubtedly serves a storage function of energy to a greater extent than either of those tissues. However, both muscle and bone serve a vital function too in storing protein and minerals in addition to fat; hence it must be questionable, whether, in studying carcass growth, one is biologically justified in treating fat as a separate entity, distinct from the rest of the carcass. The validity of doing so has been further questioned by Seebeck (1968 b).

As regards the significance of differential growth in relation to market acceptability of the carcass, there are three main criteria to consider: (1) Carcass composition in terms of bone, muscle and fat; (2) tissue distribution between the different carcass joints; and (3) the shape of the carcass. With respect to (1) growth over the normal range in slaughter age, or weight, is associated with an increase in the muscle: bone ratio; however, the major change in composition is the rising proportion of fat in the carcass, (2) Muscle weight distribution is not improved over this period; however, the proportion of the most valuable carcass muscles is only marginally reduced. In the sense that fat is being accumulated at the highest rate in the already fattest joints, the advancing fatness over the normal slaughter range can not be said to increase the uniformity of fat distribution in the carcass. However, subcutaneous fat is growing faster than intermuscular fat, which may be commercially important. The relative weight changes within the skeleton over this age interval are not per se, a matter for economic consideration. (3) As a result of changing tissue proportions and skeletal form, the carcass improves markedly in shape and appearance from the lighter end of the normal scale towards the upper limit of acceptable fatness.

Considering all these factors, it is apparent that the most important criterion is the level of fatness, which at this stage of development overshadows other developmental changes. While it is possible, by nutritional means, to modify the extent of fat deposition, associated with lean tissue growth (Elsley et al., 1964), the sheep producer has limited control over individual nutritional status; hence his easiest way of securing a high quality product is through carefully selecting his lambs for slaughter on the basis of their weight and body condition. In this respect, the present work yields information on the weight-composition relationship for the different genotypes, which should provide a valuable guideline.

The all important question, inspiring the present study, was whether breeding could improve the meat producing qualities of livestock, and more specifically what should be the place for conformation in such a breeding scheme. As already emphasized, lack of knowledge of the ultimate mature body weight of the different experimental genotypes poses a difficulty in interpreting some of the results; nevertheless, several important features have been clarified.

With respect to the growth potential, no definite conclusions can be drawn regarding the relative merits of the different types. The evidence, however, suggests that the leggier types might show an advantage, if nutrition is plentiful. The inconsistency among the Edinburgh cannon lines confuses the issue and, furthermore, the comparison may be confounded by ultimate size, as opposed to shape.

As for the qualitative aspects of growth, several outstanding features have been revealed, some of which clearly elucidate the importance of the choice of selection criteria. In general, the genotype differences in relative development were smaller in Edinburgh than in Iceland. Moreover, some of those are difficult to interpret due to the tendency for similarity of the C- and S-lines, as distinct from the L-line. Whether that likeness is a true one, or an artifact of the unbalanced experimental design, possibly influenced by non-random variation in live weight or feed consumption, can not be answered. While, generally, one would anticipate a true selection effect to be represented by approximately symmetrical deviations in each direction from the control line, there may be sound biological reasons for this not always being so; however, experimental imperfection is more likely to blame.

The most significant findings relating to genotype effects can be summarized as follows.

(1) The selection for a short cannon bone, or compact conformation, increases the weight of the carcass as a proportion of the empty body, and similarly the dressing percentage. High dressing percentage is generally considered a desirable characteristic (Pearson, 1966), since the greatest value of the animal is that of the carcass. It is important that the comparisons are not confounded by variation in kidney fat, which was excluded from the carcass; however, genotype differences in carcass fatness may be involved in the effects on dressing percentage (Seebeck and Tulloh, 1966).

(2) Linear carcass measurements revealed substantial genotype effects on external carcass form, as well as on the thickness and shape of the muscle longissimus dorsi. In this respect the outstanding feature was, that in Edinburgh, no external measurements but the length of the leg had been altered by the singular cannon bone selection, whereas in Iceland, all the criteria of carcass shape had been markedly 'improved' in the S-type, compared with the L-type. This apparent anomaly is easily

explained by the different effects that each of the selection procedures had on skeletal form and weight proportions. Increased thickness, relative to length, at all levels of the anatomy, was a characteristic achievement of the Icelandic selection method and, to a lesser extent, this was also achieved in the Edinburgh S-line. As regards the musculature, this is an important step towards improved quality. Thus, Dumont (1978), reviewing several studies of his own and others, pointed out that muscle thickness would directly affect the size of meat cuts, as well as influence meat tenderness and thus eating quality. He demonstrated a close inverse relationship between carcass fleshiness and the Warner-Bratzler shear index of its muscles, this being explained by a lower relative proportion of connective tissue in the muscles of well fleshed animals. Dumont (1978) concluded: 'It would seem that an increase in muscle thickness is in favour of most of the desirable attributes of the cattle carcass: fleshiness, conformation, muscle/bone ratio, meat texture etc'. In agreement with the present work, he also indicated skeletal form, mainly bone length, as a key to improving these various attributes.

(3) The changes brought about in carcass shape were associated with substantial genotype differences in carcass composition. Since the differences in shape were greater and more widespread in the Icelandic sheep, it was not surprising to find that so were those in composition. The Icelandic S-type was outstandingly superior to the L-type with respect to the muscle: bone ratio, which results from the massive reduction in skeletal weight (on average 22%) in the former type, compared with the latter. However, since the reduction in bone weight was associated with an increase in fat deposition, the S-type had a somewhat lower percentage of muscle than the L-type, when the two were compared at equal carcass weight. That the Edinburgh selection was less effective in changing the muscle: bone ratio is explained by its limited effect on carcass bone weight, due to the break-down of intra-skeletal weight relations.

It is important, in relation to fatness, that the main difference between the Icelandic conformation types was seen in the time of onset of fattening, rather than in the ultimate maximum rate of fat deposition. Thus, the L-type maintained a low absolute rate (g/day) of fat growth right upto weaning at 16 weeks, after which fat accumulation rose sharply;

whereas in the S-type, the increase in rate was a gradual one from birth to 24 weeks of age. To what extent this represents an inherent genetic difference, as opposed to a greater degree of early nutritional depression in the L-type, remains in doubt. What is clear, is that the S-type is more easily fattened at relatively light weights, while, under the present experimental conditions, that difference declined with increasing carcass weight.

The relative merits, in this respect, must be valued in light of practical circumstances. As far as Iceland is concerned, the sheep industry is inevitably influenced by the very short growing season. Lambs are born in May - early June and slaughtered over a period of two months in the autumn, ranging in age from 16 to 24 weeks and in carcass weight from approximately 10 to 20 kg (average of 14-15 kg).

The limits of acceptable carcass fatness are difficult to specify without a proper market survey; we can only seek support in existing guidelines. Weddell (1973) concluded, from published evidence, that back-fat thickness was a major factor in determining market acceptability of the carcass. His consultation with practising meat traders in Edinburgh further indicated that the preferred fat thickness over the L. dorsi, for lamb carcasses over the normal weight range, was 3-4 mm, with limits of acceptability of approximately 2-6 mm. The present grading system in Iceland pays a premium for carcasses of 'excellent' conformation with back-fat thickness not exceeding 4 mm. Table 9.1. shows how Weddell's (1973) optimum and acceptability limits relate to the present data in terms of carcass weight and fatness. These are mean values, around which considerable variation exists and will obviously be subject to environmental influences too. Nevertheless, they provide an indication of the problem as faced with in the practical situation.

Table 9.1. Genotype effect on the relationships between back-fat thickness, carcass weight and percentage carcass fat.[+]
A: Edinburgh.

Back-fat thickness (mm)		2	4	6
Carcass weight (kg)	Long	11.6	16.9	21.2
	Short	11.3	16.5	20.6
% carcass fat	Long	30.1	33.8	36.3
	Short	32.3	36.3	38.9

Table 9.1. (continued)

B: Iceland

Back-fat thickness (mm)		2	4	6
Carcass weight (kg)	Long	13.8	19.4	23.6
	Short	8.7	16.4	23.7
% carcass fat	Long	22.5	29.6	34.8
	Short	24.4	31.5	36.5

+) Values estimated by log-log regressions.

As far as the back-fat criterion is concerned, there appears to be little between the Edinburgh lines, despite the previous farm experience of the S-line attaining a marketable condition at the lightest weight (Purser, 1980). The Icelandic findings are of immediate practical relevance. Thus, the very early development of marketable finish must be considered a chief merit of the S-type, bearing in mind the prime objective of producing twin lambs, a high proportion of which are slaughtered at carcass weights less than 15 kg. At such weights, the virtual absence of subcutaneous fat from many of the L-type lambs, when associated with very poor conformation, is bound to result in massive down-grading of those carcasses. It is equally clear, that the S-type is more prone to exceed the 'optimal' level of fatness at high carcass weights though within the normal range. In this respect, however, one important point must be made. Within the S-type, there was considerable variation in fatness at any stage of growth. There was no indication of excessive fatness being associated with the most superior carcass form. Indeed, some of the best shaped S-carcasses contained the least amount of fat (see e.g. no. 1047 in plate 5.1.), but were characterized by a short skeletal structure with thick muscling and a high proportion of their fat subcutaneously. Within type analysis failed to reveal any significant correlations between percentage carcass fatness and such criteria of conformation as T, F, F-T, or G/T at constant carcass weight. The excessive fatness of some S-type lambs would appear to have resulted from the occasional failure in the selection procedure to acknowledge the disguising effect that fat may have on conformation, judged in the live animal. Overcoming that, there seems to be no biological objection to the achievement of superior carcass form, in terms of thick muscling and a high ratio of muscle to bone, at any weight within the normal range, without the detriment of wasteful fatness.

(4) Each of the two selection procedures produced marked genotype differences in the relative proportions of the various carcass joints. Contrary to the belief of some workers (Kirton and Pickering, 1967), these were associated, not only with the movement of fat, but no less with changes in the distribution of muscle and bone in the carcass. Probably the most significant achievement was the proportional increase in back-muscles in the Icelandic S-type (11% in 1. dorsi, 12% in prime loin muscle, compared with the L-type) at the expense of fore quarter muscles.

The magnitude of this difference must be considered of economic importance, provided that carcass grading is sound so that the producer gets paid on a qualitative basis. Furthermore, the progress so far must be valued in light of the relatively short time span (25 years), over which it has been achieved. Available evidence suggests that there is still scope for continuing progress in this field. Thus, the coefficients of variation of individual muscle groups as percentage of total muscle, within type and after adjustment for weight and sex, ranged from 3.0% to 5.3%. That amount of variation has been considered appreciable for selection purposes (Jackson, 1969).

Finally, the most important conclusion from the present study, and the most controversial, has to be that none of the characteristics under consideration, neither tissue interrelationships nor intra-tissue proportions, are too rigid in nature not to be modified by the animal breeder, if so desired. The fact that breeding attempts are frequently reported to have been unsuccessful in altering tissue proportions (e.g. Berg and Butterfield, 1976) is probably due more to misjudged criteria of superiority than to the genetic or functional impossibility of improving these. The potential seems to exist; the progress will largely be subject to economic priorities.

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APPENDIX 1.

DIET EVALUATION.

Two balance trials were undertaken to evaluate the diet, using 12 Blackface wether lambs in both trials. Initially the lambs were chosen to be similar in weight to the growth trial lambs and were fed to make similar weight gains between the two trials. The 12 lambs were allocated to each of three feeding planes in the same way as for the main trial. Levels of feeding were set in accordance with intakes on the growth trial and are shown in table A.1.1.

Due to the incidence of urinary calculi, the diet had to be changed between the two trials. The change involved the reduction of barley from 90% to 85%, this being met by an increased proportion of the protein supplement and the inclusion of salt and limestone. Consequently, the composition of Diet 2 was somewhat different from that of Diet 1. (table A.1.3.).

In both trials the lambs were harnessed in metabolism crates and their faeces and urine collected over a ten day feeding period, preceded by a period of at least seven days 'acclimatisation'. During the collection period, feed residues were collected daily (when present), weighed and sampled for analysis. The lambs were weighed before and after each trial.

Calculations of digestibilities and metabolizable energy values were carried out according to McDonald, Edwards and Greenhalgh (1966), making corrections for methane losses using the formula of Blaxter and Clapperton (1965).

Results. Daily rations, intakes and live weights of the lambs are shown in tables A.1.1. and A.1.2. In neither trial did all the lambs eat up their rations, which somewhat upset the relative plane differences. This was most marked on H-plane in Trial 2, the deviation being caused by low intakes of two lambs. However, as estimates of coefficients for these lambs fell within those of the other two there is no reason for excluding them from the analysis.

Diet compostition, as analysed in the laboratory, is presented in table A.1.3. The main differences between the two diets lie in the proportions of ash and organic matter and the higher crude protein content of Diet 2. The difference in gross energy between the two diets was smaller than between repeated measurements of the same diet, and can therefore be ignored.

It is apparent from table A.1.4. that there was a trend for digestibility coefficients to fall with increasing level of intake in Trial 1, while this was less systematic in Trial 2. The differences were, however, non-significant for the number of lambs employed.

While the apparent digestibility coefficients for dry matter, organic matter and energy were similar in both trials, the difference in protein digestibility was close to statistical significance. This difference can most likely be explained by the higher protein content of Diet 2, as several workers have shown that increasing the protein concentration tends to increase the apparent digestibility of crude protein (Robinson and Forbes, 1966, 1967, 1970; Mansour, 1969; Andrews and Ørskov, 1970).

Table A.1.5. shows the concentrations of metabolizable energy and digestible crude protein in the two diets as estimated in trials 1 and 2. The significantly higher content of DCP in Trial 2 reflects the greater CP content of diet 2 and has probably no relation to the maturity stage of the lambs. Differences due to feeding plane were negligible and so was the diffenence in ME value between diets 1 and 2. It thus appears safe to assume common values of ME and DCP for all three feeding planes in our growth trial regardless of age or weight of the lambs.

Table A.1.1. Daily allowances and intakes.

Plane	Trial 1		Trial 2	
	Ration (gDM)	Intake (gDM)	Ration (gDM)	Intake (gDM)
H	727	722 ± 5.0	1091	957 ± 80.0
M	654 (90)*	612 ± 25.9 (85)	982 (90)	942 ± 3.7 (98)
L	547 (75)	512 ± 35.5 (71)	818 (75)	776 ± 41.8 (81)

* Figures in brackets indicate % of H.

Table A.1.2. Live weights of lambs.

Plane	Trial 1 Pre-trial (kg)	Trial 1 Post-trial (kg)	Trial 2 Pre-trial (kg)	Trial 2 Post-trial (kg)
H	24.1 ± 1.30	26.4 ± 1.22	49.6 ± 1.93	50.3 ± 1.93
M	22.3 ± 1.50	24.0 ± 1.81	46.5 ± 2.54	47.6 ± 2.67
L	22.7 ± 1.15	23.6 ± 1.04	47.1 ± 1.51	48.3 ± 1.23

Table A.1.3. Dietary composition - Laboratory analysis.

Component		Diet 1	Diet 2
Dry matter (DM)	g/100g	85.5	83.9
Ash	g/100g DM	5.6	9.2
Organic matter (OM)	"	94.4	90.8
Fat	"	1.7	1.9
Fibre (TCA)*	"	5.3	4.8
Crude protein (CP)	"	14.2	15.6
Gross energy	KJ/gDM	17.9	17.7

* TCA = Tri-chloro acetic acid.

Table A.1.4. Apparent digestibility coefficients for dry matter, organic matter, crude protein and energy (mean values & standard errors).

A. Trial 1.

Plane	DM	OM	CP	GE
H	0.812 ± 0.0101	0.829 ± 0.0100	0.740 ± 0.0169	0.808 ± 0.0110
M	0.817 ± 0.0152	0.834 ± 0.0150	0.743 ± 0.0195	0.813 ± 0.0172
L	0.824 ± 0.0079	0.843 ± 0.0080	0.743 ± 0.0290	0.815 ± 0.0102
Mean	0.818 ± 0.0066	0.835 ± 0.0066	0.742 ± 0.0129	0.812 ± 0.0076

B. Trial 2.

Plane	DM	OM	CP	GE
H	0.803 ± 0.0061	0.835 ± 0.0057	0.787 ± 0.0097	0.821 ± 0.0067
M	0.800 ± 0.0080	0.834 ± 0.0076	0.765 ± 0.0240	0.820 ± 0.0098
L	0.803 ± 0.0112	0.842 ± 0.0069	0.777 ± 0.0066	0.828 ± 0.0077
Mean	0.802 ± 0.0050	0.837 ± 0.0039	0.776 ± 0.0089	0.823 ± 0.0047

Table A.1.5. Estimated contents of metabolizable energy and digestible crude protein (mean values and standard errors).

Plane	ME (kJ/gDM)		DCP (g/100gDM)	
	Trial 1	Trial 2	Trial 1	Trial 2
H	12.5 ± 0.16	12.3 ± 0.15	10.5 ± 0.24	12.3 ± 0.15
M	12.5 ± 0.24	12.2 ± 0.07	10.6 ± 0.23	11.9 ± 0.37
L	12.6 ± 0.17	12.4 ± 0.13	10.6 ± 0.41	12.1 ± 0.10
Mean	12.5 ± 0.11	12.3 ± 0.07	10.6 ± 0.18	12.1 ± 0.14

APPENDIX 2.

SEPARATION OF BODY COMPONENTS AT SLAUGHTER.

The following offals were removed and weighed (to the nearest 1 - 0.01 g) at slaughter. Only those parts indicated by an 'E' were recorded separately in Edinburgh.

Blood (E)

Head (E) - disarticulated at the atlanto - occipital joint

Feet (E) - severed between metacarpus/metatarsus and carpals/tarsals.

Pelt (E)

Total thoracic organs (E)
- Thyroids
- Neck thymus
- Heart thymus
- Heart (E)
- Lungs + trachea
- Pericardium + blood vessels + waste
- Diaphragm

Alimentary tract (E) (full and empty)
- Oesophagus
- Rumen
- Reticulum
- Omasum
- Abomasum
- Small intestine
- Caecum
- Colon + rectum

Liver (E)

Gall bladder (full and empty)

Caul fat

Mesenteric fat

Pancreas

Spleen

Urine bladder

Penis + retractor penis muscle

Testes

Ovaries

Uterus + oviducts + vagina.

APPENDIX 3.

LINEAR MEASUREMENTS.

3.a. Carcass measurements.

The measurements described below are illustrated in figure A.3.1.

T - length of tibia + tarsus from the tubercle on the proximal end of the tibia to the anterior edge of the distal end of the tarsus.

F - Inside leg length.

G - Width of gigots.

TH- Depth of thorax. The maximum depth of the chest behind the shoulders.

V - Width of thorax. The minimum width of the chest behind the shoulders.

W - Width of shoulders. The maximum width over the shoulders.

L - Length of trunk from the symphisis pubis to the anterior edge of the distal end of the first rib.

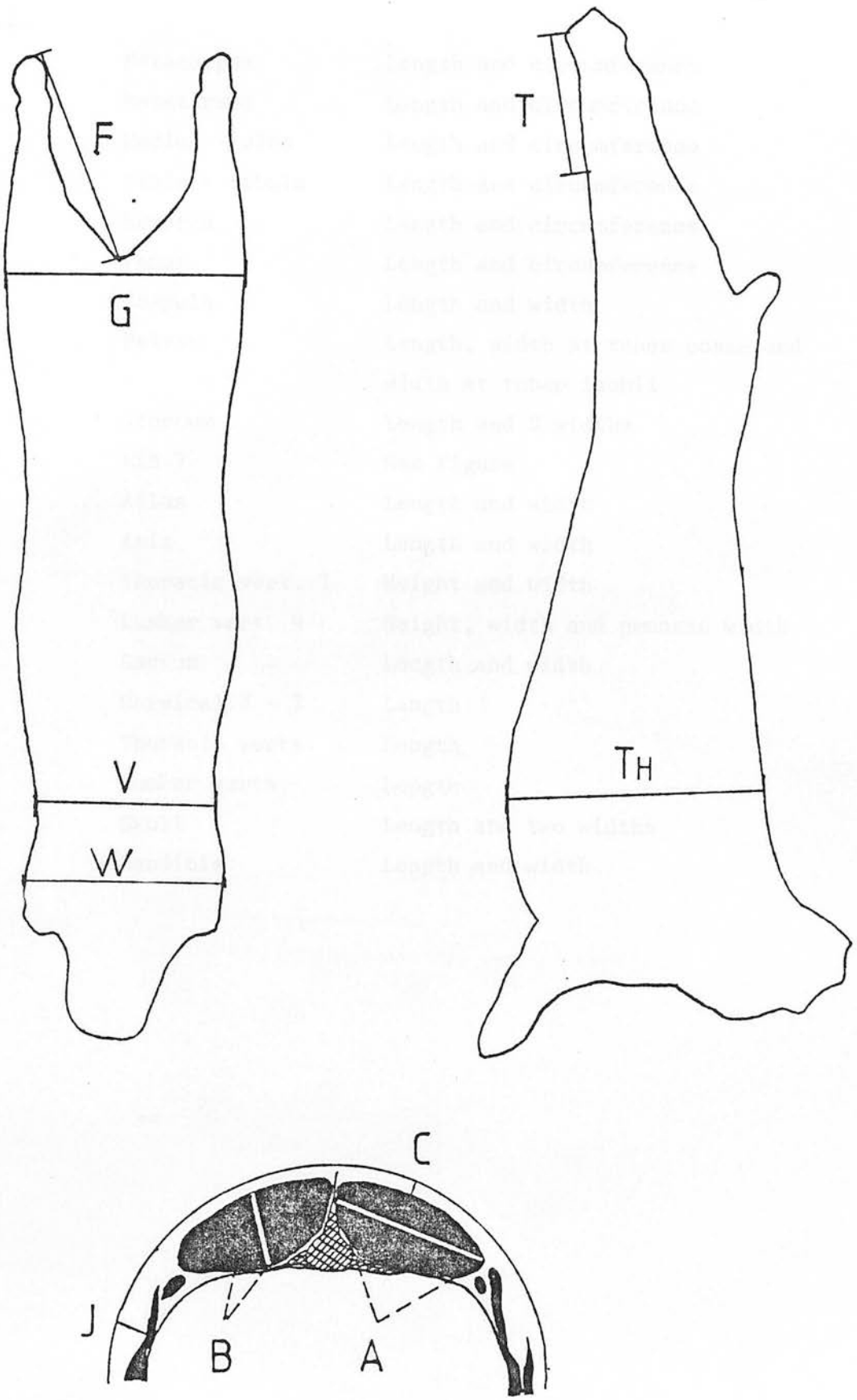
A - Length of eye muscle. The maximum distance across the crossection surface of the longissimus dorsi muscle at the 12th rib.

B - Depth of eye muscle. The greatest distance at right angles to A on the same surface.

C - Back-fat thickness over the deepest part of the eye muscle.

J - Thickest layer of fat over rib.

Figure A.3.1. Carcass Measurements.



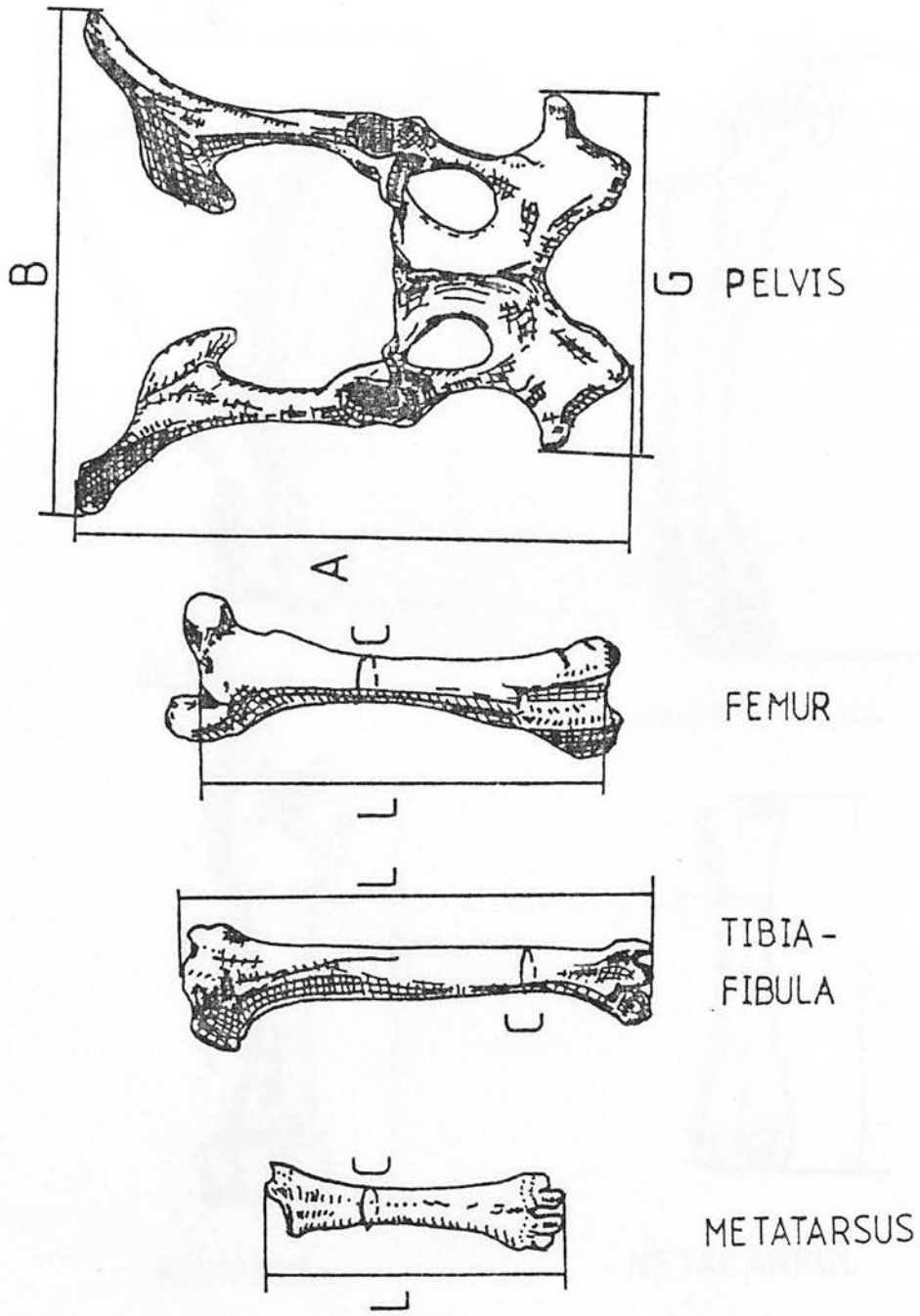
3.b. Measurements of skeletal dimensions.

A total of 43 measurements were rocorded of different bone dimensions. These are summarized below and illustrated in figure A.3.2.

Metacarpus	Length and circumference
Metatarsus	Length and circumference
Radius - ulna	Length and circumference
Tibia - fibula	Length and circumference
Humerus	Length and circumference
Femur	Length and circumference
Scapula	Length and width
Pelvis	Length, width at tuber coxae and width at tuber ischii
Sternum	Length and 2 widths
Rib 7	See figure
Atlas	Length and width
Axis	Length and width
Thoracic vert. 7	Height and width
Lumbar vert. 4	Height, width and process width
Sacrum	Length and width
Cervical 3 - 7	Length
Thoracic verts.	Length
Lumbar verts.	Length
Skull	Length and two widths
Mandible	Length and width.

Figure A.3.2. Bone Measurements.

A: Hind limb.

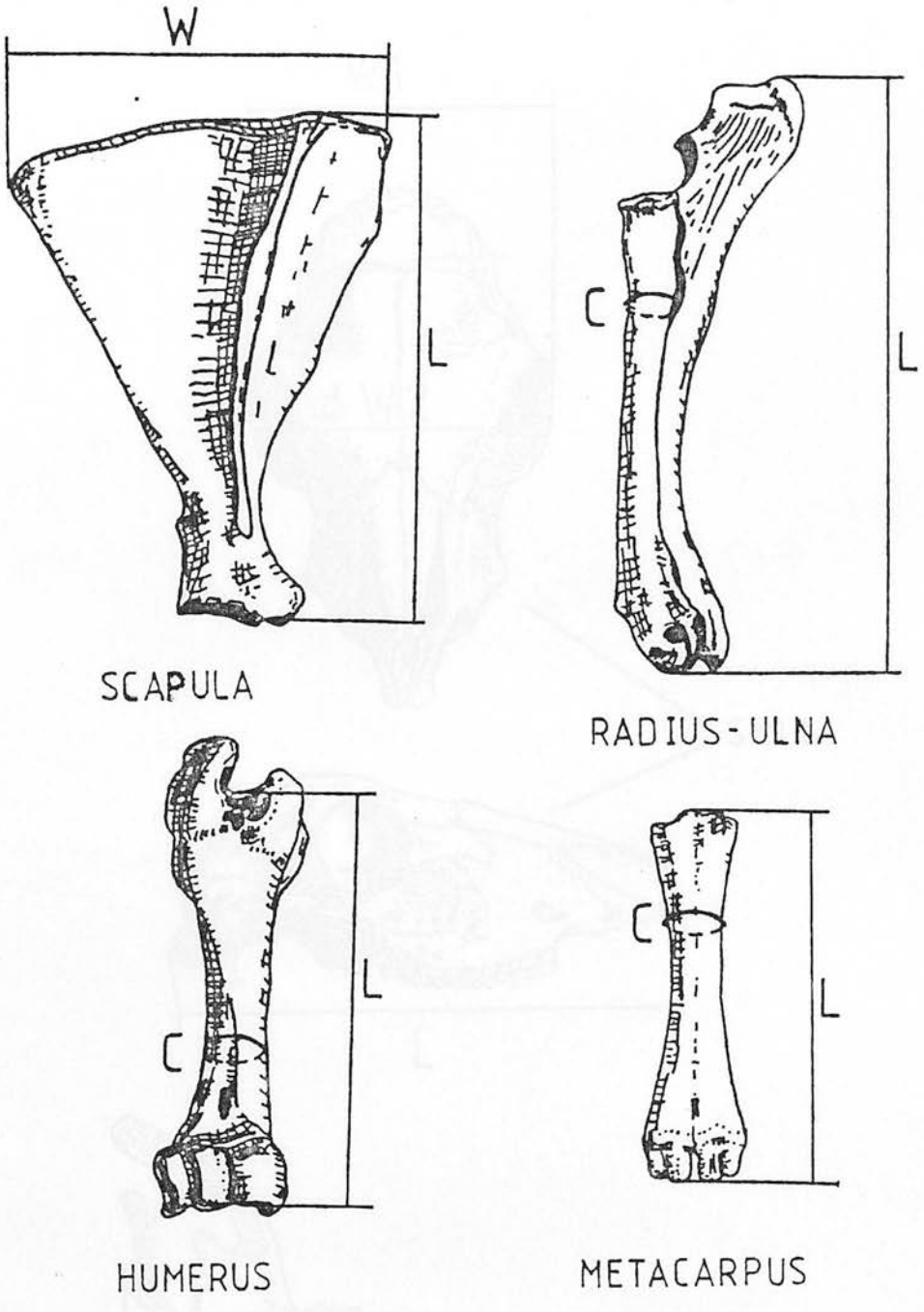


A: Length
B: Width at tuber coxae
G: Width at tuber ischii

L: Length
C: Circumference

Figure A.3.2. (Continued)

B: Fore limb.



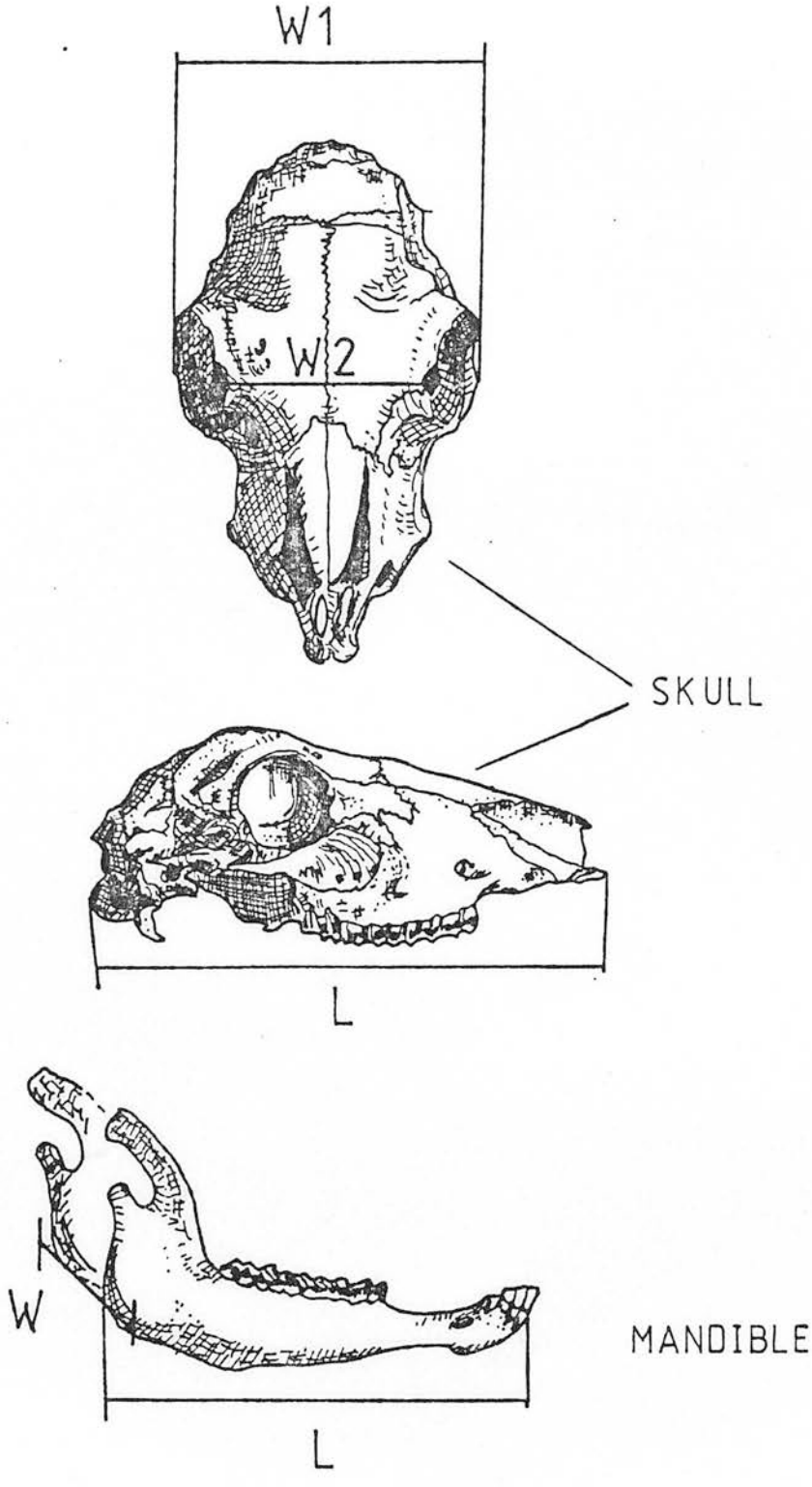
L: Length

C: Circumference

W: Width

Figure A.3.2. (Continued)

C: Head.



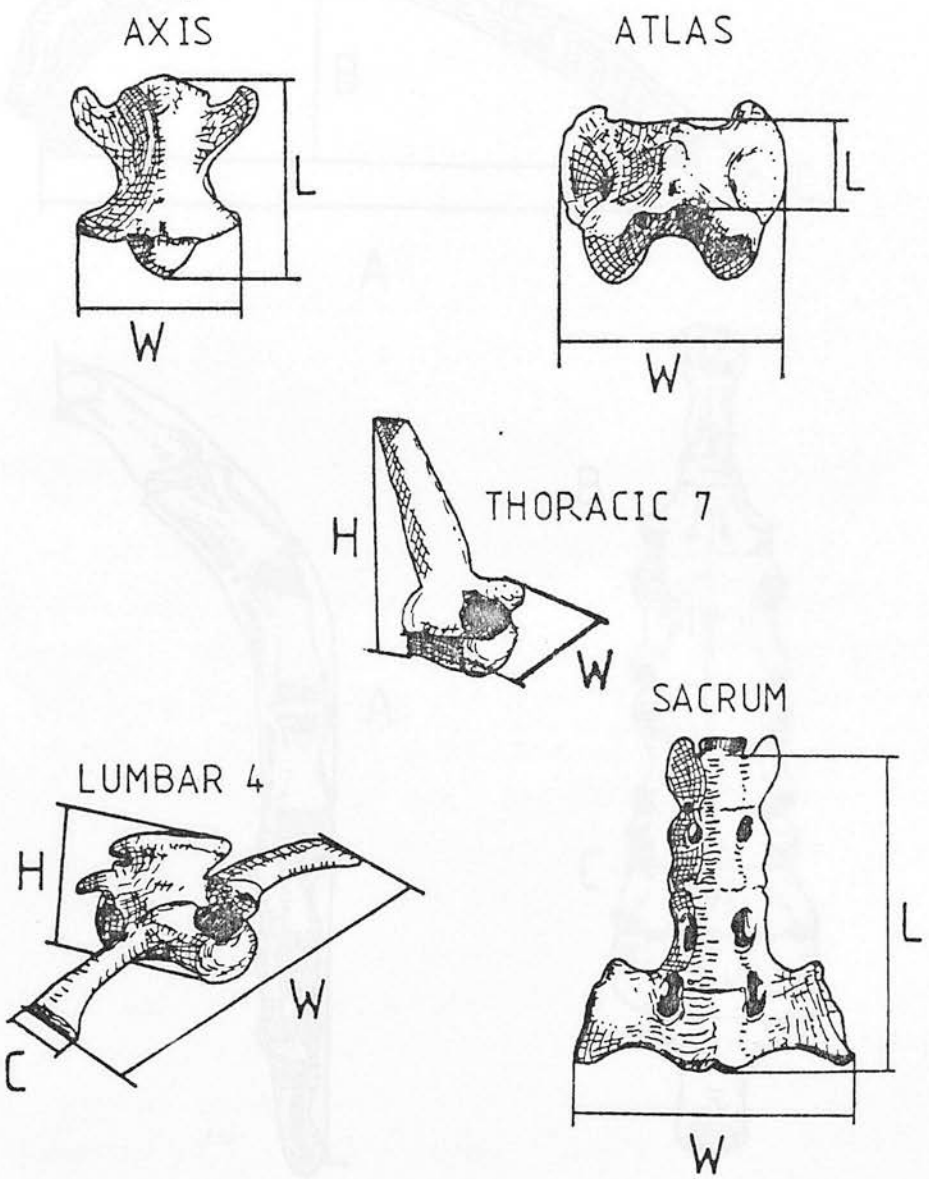
L: Length

W1: Max. width over eyes

W2: Min. width over eyes

Figure A.3.2. (Continued)

D: Vertebrae.



L: Length of vertebral body

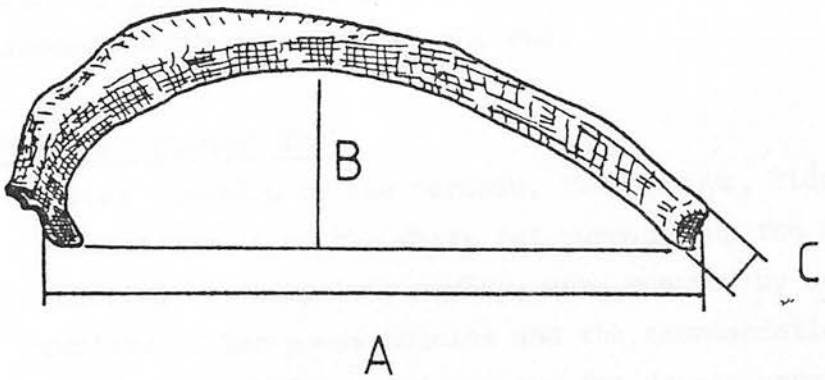
W: Width of body + transverse processes

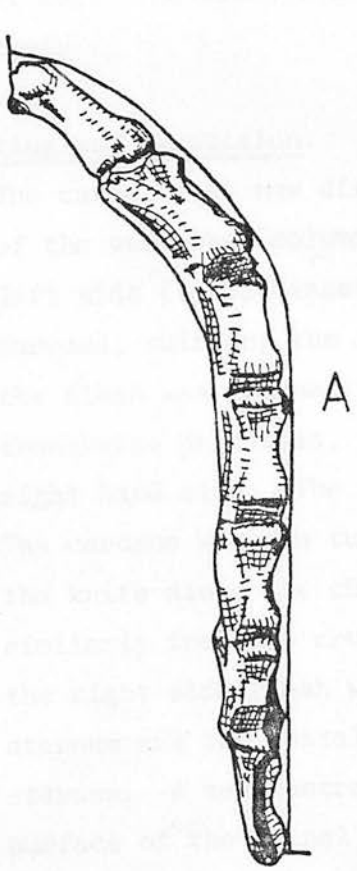
H: Height of body + spinal process

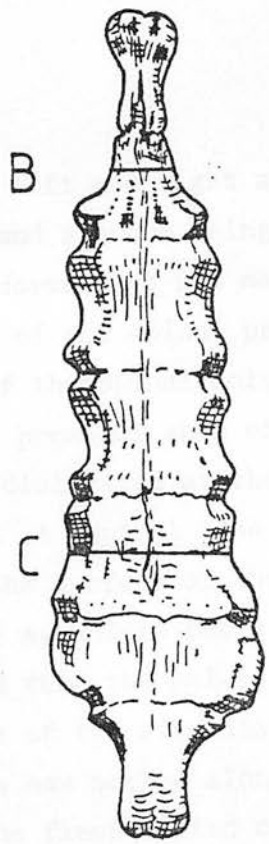
C: Width of transverse process

Figure A.3.2. (Continued)

E: Rib and sternum.







RIB 7:

A: Distance between extremities

B: Maximum spring

C: Width at sternal extremity

STERNUM:

A: Curved length

B: Width (second segment)

C: Width (third segm. from post. end)

APPENDIX 4.

CARCASS JOINTING PROCEDURE AND TISSUE SEPARATION.

The splitting of the carcass and the separation of the major retail cuts was identical in both trials, while further division into primary and secondary joints was different for each trial. The following procedure refers to the Icelandic work, the deviations in Edinburgh being described at the end.

Kidney and channel fat.

1. Before division of the carcass, the kidneys, kidney fat and channel fat, i.e. the white fat surrounding the kidneys, and adhering to the pelvic cavity, were removed by scraping the surface of the psoas muscles and the sacrosciatic ligament free of fat. The kidneys and the two fat depots were recorded separately.

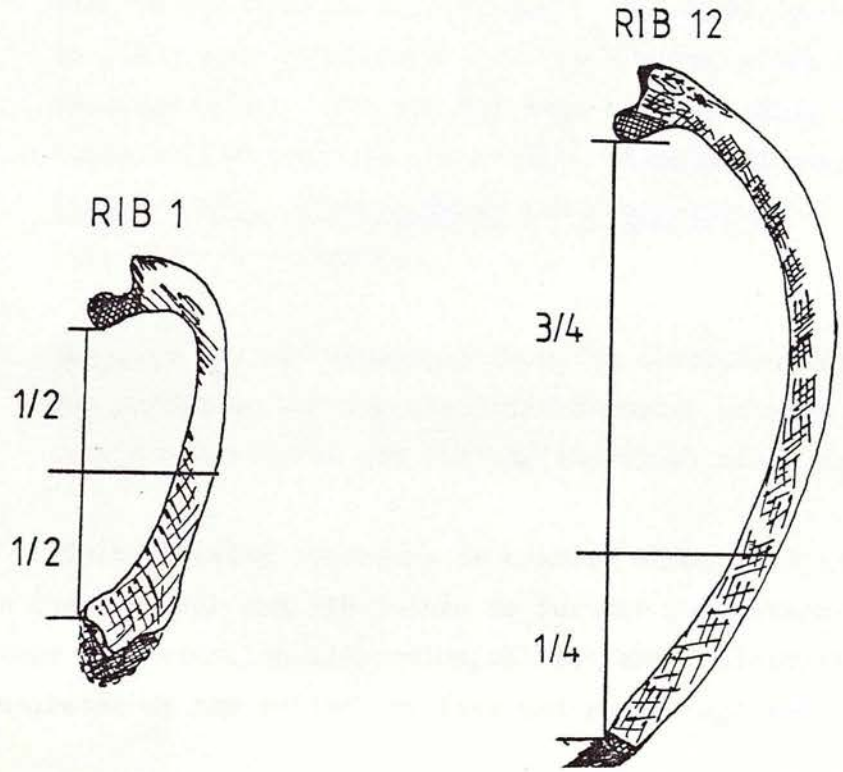
Jointing and dissection.

2. The carcass was now divided into left and right sides, the whole of the vertebral column, pelvis and sternum being included in the left side (to be dissected). A dorsal cut was made along the carcass, skirting the right side of the spinal processes. Thus the flesh was gradually lifted of the spinal column exposing the transverse processes, pelvis and proximal ends of ribs on the right hand side. The femur was dislocated at the pelvic joint. The carcass was now turned over. A central line was marked with the knife along the chest into the surface of the sternum and similarly from the crutch to the symphisis pubis. Step by step the right side flesh was removed from the pelvis, sacrum and sternum and the costal processes of the ribs dislocated from the sternum. A new central line was now marked along the ventral surface of the spinal column, the flesh lifted off and the ribs dislocated from the thoracic vertebrae. This allowed the completion of the longitudinal division, after which each side was weighed separately.

3. A deflanking line to mark the longitudinal division between the dorsal (primary joints) and ventral (secondary joints) parts of

Figure A.4.1. Splitting of the Carcass.

Figure A.4.2. Deflanking Points on Ribs.
(Iceland)



the side was marked on the inside of the rib cage from a point half the length of the first rib to a point three quarters of the distance on the twelfth rib (see figure A.4.2.). From there the line was continued along the flank, the ruler being placed ventrally on the symphisis pubis. A scalple was inserted at right angles between the ribs and trough the flank to mark the line on the outside, before any joints were cut.

4. The gigot was removed by inserting a knife ventrally between the two last lumbar vertebrae and cutting the flesh along the line of the knife's incision, but not through the tuber coxae. The piece of flank removed from the gigot, contained parts of the muscles obligus abdominis internus, rectus abdominis and pamiculus carnosus, together with fat, including the cod/udder fat. The dividing line followed the ventral edge of the muscle tensor fasciae latae.

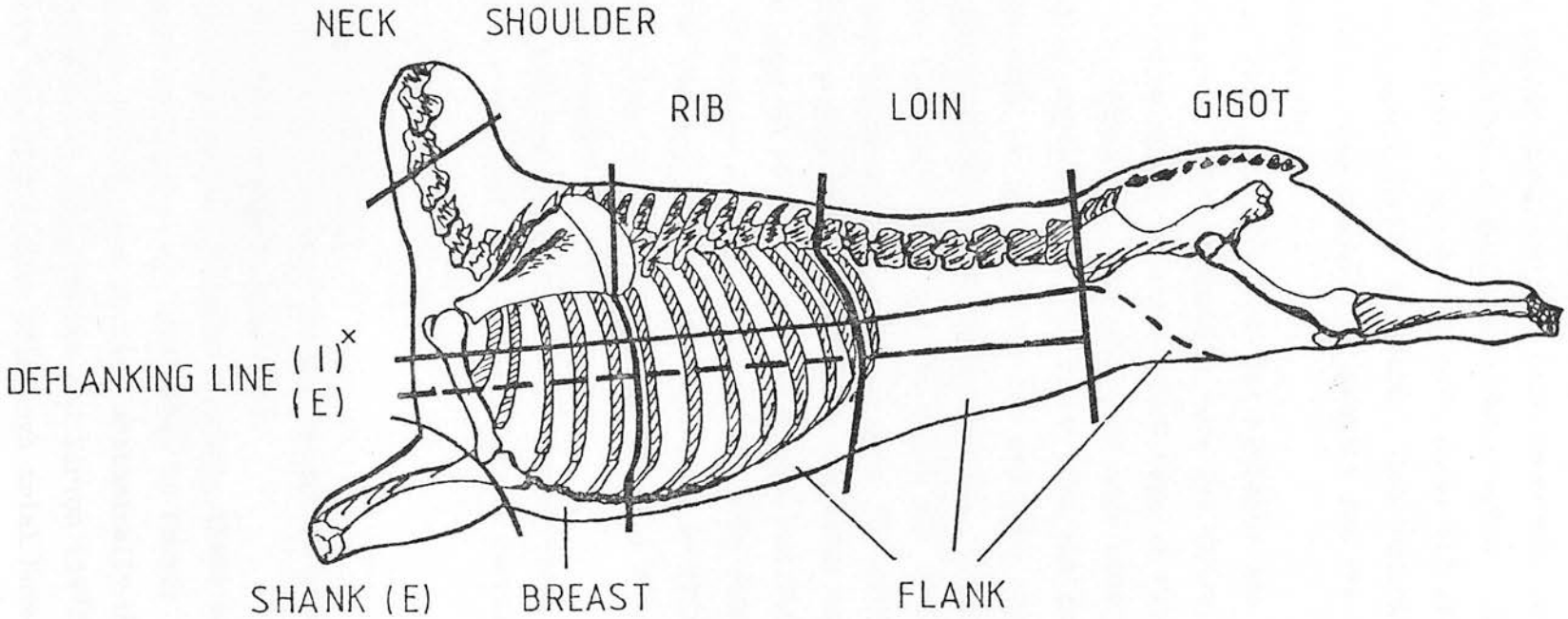
5. The loin was cut off between the 12th and 13th ribs, the knife crowding the 12th rib and finally separating the 12th and 13th thoracic vertebrae. the flank was cut off the loin along the previously described line.

6. The rib joint was separated from the shoulder between thoracic vertebrae 5 and 6, the knife being projected ventrally skirting the 5th rib down to the sternum. The costal processes, posterior to rib 5, were dismantled from the sternum which remained in the shoulder joint. The cut was made without going through the scapulae cartilage or the closest associated muscles (supraspinatus, infraspinatus, subscapularis and rhomboideus) all of which were left with the shoulder.

7. The neck was not separated from the shoulder, but the division was marked by pushing the knife dorsally between the 3rd and 4th cervical vertebrae and cutting the flesh along that line.

This jointing procedure is coarsly summarized in figure A.4.3. In the shoulder and rib joints no further separation was done at this stage. However, on dissection, all fat and individual muscles were separated at the deflanking line and recordings made accordingly.

Figure A.4.3. Jointing of the Carcass.



x) I: Iceland, E: Edinburgh.

After jointing separation of tissues and individual muscles was carried out, following the procedure of Fourie (1962, 1965), except in two cases where confidence over the separation of muscles could not be established and these were grouped together. In this way 69 individual muscle or muscle group weights were recorded, compared with 76 by Fourie. All bones were scraped clean and weighed. The sacral and coccygeal vertebrae were weighed as a unit while all other vertebrae and ribs were individually recorded. Bone scrapings were weighed separately and so were tendons + ligaments and the spinal cord and its surrounding fat.

In the Edinburgh trial, the division into primary and secondary joints was done as follows: The deflanking line was drawn, as by Jackson, from the anterior point of the ventral edge of rib 1 to the ventral edge of rib 13. This line was projected back over the loin region and only used to separate the loin flank from the prime loin. No sub-divisions were made of the gigot or rib and only the neck and shank were cut off the shoulder as secondary joints. The neck was taken off at the same line as before and the shank was dislocated at the elbow joint, the flesh being cut along a line over the proximal edge of the ulna, marked by a pair of dividers with the other arm held at the anterior distal edge of the carpals (see figure A.4.3.).

All standards of separating and cleaning the main tissues were set the same for both trials, as well as could be. In this trial, however, only 14 individual muscles were recorded, all other muscles from each joint being weighed in bulk.

In addition to recording bone weights for each joint, all limb bones were individually weighed, as well as selected sample bones from the trunk.

4.c. Individual muscle dissection.

The following individual muscles or muscle groups were dissected out of the joints and their weights cumulated.

A comprehensive description of these muscles, their anatomical locations, attachments and functions, was given by Fourie (1962, 1965). The muscles are listed here in nine anatomically defined groups, the same as those of Jury, Fourie and Kirton (1977). The 14 muscles, individually recorded in the Edinburgh trial have been identified by an 'E'.

1. Muscles of the hind limb - proximal part (15).

Tensor fasciae latae
Biceps femoris
Gluteus medius (E)
Semitentinosus (E)
Quadriceps femoris (E)
Gluteus accessorius
Gluteus profundus
Gemellus
Quadratus femoris
Gracilis
Sartorius
Pectineus
Semimembranosus (E)
Adductor femoris
Oburators externus + internus

2. Muscles of the hind limb - distal part (7)

Gastrocnemius (E)
Soleus
Extensor digitorum lateralis
Peroneus longus
Peroneus tertius + extensor group
(Extensor digitorum longus - E)
Tibialis anterior
Flexor group

3. Muscles surrounding the spinal column (6)

Iliacus
Psoas major (E - loin only)
Psoas minor (E - loin only)
Quadratus lumborum
Longissimus dorsi (E - loin, rib, shoulder)
Multifidus dorsi

4. Abdominal muscles (6)

Panniculus carnosus (cutaneous)
Serratus dorsalis caudalis

Obliqus abdominis externus
Rectus abdominis
Obliqus abdominis internus
Transversus abdominis

5. Muscles of the fore limb - proximal part (11)

Deltoideus
Tensor fasciae antibrachii
Infraspinatus (E)
Teres minor
Supraspinatus (E)
Subscapularis
Coracobrachialis
Teres major
Triceps brachii
Biceps brachii (E)
Brachialis (E)

6. Muscles of the fore limb - distal part (2)

Flexor group
Extensor group
(extensor carpi radialis - E)

7. Muscles joining fore limb to neck (4)

Trapezius cervicalis
Brachiocephalicus
Omotransversarius
Serratus ventralis

8. Muscles joining fore limb to thorax (3)

Latissimus dorsi
Pectoralis profundus + superficialis
Rhomboideus

9. Muscles of neck and thorax (15)

Scalenus dorsalis
Sternocephalicus + sternothyrohyoideus
Splenius
Scalenus ventralis + rectus capitis ventralis
+ omo-hyoideus

Longissimus capitis et atlantis

Complexus

Rectus capitis dorsalis major

Obliqus capitis posterior

Serratus dorsalis cranialis

Transversus thoracic

Longissimus costarum

Longus colli

Intraversales colli

Multifidus cervicis

Intercostales

APPENDIX 5.

DISSECTION OF THE HEAD AND FEET.

Head. The dissection procedure involved separating, cleaning and weighing the following parts: Horns, skin, eyeballs, skull, mandible, hyoid bone and brain.

1. The horns (when present) were removed by inserting a strong knife between the processus cornus and the surrounding hornlayer. By cutting through the horn as required and applying force at the same time, the horns could be removed, leaving the processus cornus intact with the skull. Remaining connective tissue was scraped off and weighed with horns.

2. The skin was removed of the head by the aid of a scalple and weighed.

3. The eyeballs were carefully loosened from the sockets by incisions through the eyelids and severing of fascia bulbi, optical nerve and oculor muscles. They were trimmed, cleaned and weighed.

4. The mandible was dislocated from the head, scraped clean and weighed.

5. The hyoid bone was taken out, scraped and weighed.

6. The skull was scraped as clean as possible, while intact, and weighed after removal of the brain.

7. The brain was removed and weighed. To reach the brain, a fine saw was used and a cut made round the skull posterior to the processus cornus and anterior to the paramastoid process. After removal of the skull cap, the brain was removed, care being taken not to leave any parts behind.

8. No distinction was made between other tissues or parts of the head; they were weighed together with the scrapings as soft tissue.

Feet. The skin, hooves, metacarpus/metatarsus, proximal, medial and distal phalanges, proximal and distal sesmoids were all separated, cleaned and weighed. Tendons, ligaments and bone scrapings were weighed together.

APPENDIX 6.

LEAST-SQUARES ANALYSIS OF VARIANCE OF CARCASS COMPOSITION.[+]

F-VALUES.

Source of variation	Degr. of freed.	Muscle	Bone	Subcut. fat	Intermusc. fat
A: Edinburgh (On trial)					
Group [x]	1	8.36	3.99	8.75	13.11
Cannon line	2	5.12	9.83	10.30	1.71
Regressions:					
On carc. wt. - linear	1	718.83	341.16	521.15	206.75
" " " - quadratic	1	3.66	9.14	7.37	3.60
On daily D.M. intake-linear	1	6.07	1.40	6.27	7.65
Residual mean square	91	0.00055	0.00080	0.00297	0.00187
B: Iceland (Birth - 24 weeks)					
Conformation type	1	17.79	167.20	21.54	17.75
Sex	1	3.44	7.92	7.09	5.98
Type of birth	1	0.13	22.41	2.34	0.41
Regressions:					
On carc. wt. - linear	1	1155.73	383.58	320.49	533.93
" " " - quadratic	1	39.07	9.71	15.64	9.60
Interactions:					
Conf. type x regr. linear	1	0.02	4.72	3.77	1.85
Sex x " "	1	0.00	0.49	1.16	0.04
Type of birth x " "	1	1.55	3.28	3.90	2.04
Conf. type x regr. quadratic	1	1.41	1.90	6.56	5.36
Sex x " "	1	0.14	1.84	1.87	0.06
Type of birth x " "	1	1.58	2.22	2.73	3.22
Residual mean square	52	0.00029	0.00046	0.00681	0.00260

+) Analysis undertaken on log-transformed tissue and carcass weights and the main effects contrasted at 16.0 kg carcass weight.

x) Two groups, i.e. the initial slaughter group (8 lambs) and all lambs on the feeding trial, except maturity group (90 lambs).

APPENDIX 7.

RELATIVE GROWTH COEFFICIENTS, RELATING BODY COMPONENTS TO PELT-FREE EMPTY BODY WEIGHT. (ICELAND).

- Adjusted for conformation type, sex and type of birth.

Component	I Age: 0-6 wks. b	SE	II Age: 6-16 wks. b	SE	III Age: 16-24 wks. b	SE	IV Age: 48-74 wks. b	SE	Signific.of b-differences† I-II	II-III	III-IV
Carcass	1.05	0.013	0.98	0.027	1.04	0.057	1.30	0.100	N.S.	N.S.	*
Head	0.63	0.015	0.78	0.021	0.81	0.113	0.90	0.221	***	N.S.	N.S.
Feet	0.49	0.021	0.48	0.024	0.63	0.060	0.68	0.075	N.S.	N.S.	N.S.
Pelt	0.74	0.031	1.03	0.048	1.45	0.158	2.63	0.584	**	*	N.S.
Blood	0.77	0.032	0.87	0.044	0.90	0.136	(0.45)	0.309	N.S.	N.S.	N.S.
Liver	1.06	0.051	0.76	0.039	1.31	0.165	0.57	0.181	**	*	*
Spleen	1.31	0.054	0.35	0.097	1.12	0.162	(0.75)	0.379	***	**	N.S.
Pancreas	1.30	0.054	1.11	0.100	0.77	0.205	(0.78)	0.379	N.S.	N.S.	N.S.
Thyroid	0.71	0.088	(0.20)	0.153	1.85	0.594	(-0.76)	0.654	*	*	*
Neck thymus	1.26	0.098	(-0.46)	0.243	(-0.20)	0.794	-2.88	0.905	***	N.S.	N.S.
Heart thymus	1.04	0.179	1.09	0.245	(0.10)	0.533	(0.46)	1.017	N.S.	N.S.	N.S.
Pericardium +	0.85	0.096	1.22	0.144	1.48	0.377	1.92	0.415	N.S.	N.S.	N.S.
Heart	0.85	0.034	0.79	0.045	0.82	0.123	0.94	0.145	N.S.	N.S.	N.S.
Lungs + trachea	0.70	0.025	0.46	0.054	0.75	0.164	(0.03)	0.212	**	N.S.	N.S.
Diaphragm	0.99	0.056	1.17	0.042	0.84	0.113	0.82	0.155	N.S.	*	N.S.
Tot. thor. orgs.	0.83	0.016	0.68	0.043	0.86	0.136	0.64	0.126	**	N.S.	N.S.
Kidneys	0.93	0.033	0.54	0.050	0.83	0.142	(0.22)	0.194	***	N.S.	N.S.
Gall bladder	0.86	0.107	1.27	0.204	1.17	0.397	(1.66)	0.620	N.S.	N.S.	N.S.
Urine bladder	0.17	0.056	0.35	0.082	1.52	0.422	1.28	0.177	N.S.	*	N.S.
Penis +	0.99	0.115	1.09	0.152	0.99	0.215	1.10	0.300	N.S.	N.S.	N.S.
Testes	1.05	0.177	2.83	0.357	1.37	0.326	2.36	0.904	**	*	N.S.
Uterus + vagina	0.64	0.104	0.44	0.171	1.00	0.243	(-0.40)	0.295	N.S.	N.S.	*
Ovaries	1.47	0.160	1.13	0.327	(0.35)	0.368	1.99	0.888	N.S.	N.S.	N.S.
Oesophagus	1.13	0.031	1.02	0.082	(0.77)	0.541	0.63	0.198	N.S.	N.S.	N.S.
Rumen	2.27	0.046	1.79	0.059	0.65	0.178	1.11	0.260	***	***	N.S.
Reticulum	1.85	0.072	1.46	0.066	0.79	0.137	0.62	0.254	**	**	N.S.
Omasum	1.52	0.077	2.09	0.121	(0.29)	0.345	1.40	0.439	*	***	N.S.
Abomasum	1.08	0.046	0.87	0.104	(0.36)	0.220	1.77	0.268	N.S.	*	**
Small intest.	1.75	0.048	0.24	0.072	(0.16)	0.179	0.58	0.232	***	N.S.	N.S.
Caecum	1.82	0.051	1.19	0.125	(0.74)	0.536	1.78	0.538	**	N.S.	N.S.
Colon + rectum	1.73	0.064	1.22	0.120	(0.38)	0.412	(0.32)	0.252	**	N.S.	N.S.
Tot.alim.tract	1.72	0.030	0.91	0.052	0.45	0.141	0.85	0.141	***	*	*
Caul fat	2.13	0.175	2.82	0.226	2.23	0.339	2.18	0.395	N.S.	N.S.	N.S.
Mesent.fat	1.81	0.116	1.54	0.073	1.63	0.256	2.62	0.420	N.S.	N.S.	*
Kidney fat	0.68	0.143	2.71	0.183	1.73	0.290	3.08	0.629	***	*	N.S.
Cannel fat	0.71	0.143	1.93	0.195	1.78	0.516	2.32	0.934	**	N.S.	N.S.

+) Differences between b-values in age intervals I & II, II & III and III & IV, respectively.

- Values in parentheses are non-significant from zero.

APPENDIX 8.

THE WEIGHTS OF VARIOUS NON-CARCASS COMPONENTS AT CONSTANT PELT-FREE EMPTY BODY WEIGHTS.

Table A.8.1. Edinburgh.

Component	Line	Pre-trial; PFEB = 10 kg						On trial; PFEB = 30 kg+					
		Mean (g)	SE	Signific.of difference L-C	L-S	C-S	Relat. diff. (C=100)	Mean (g)	SE	Signif.of difference L-C	L-S	C-S	Relat. diff. (C=100)
Carcass	L	5892	104	N.S.	N.S.	N.S.	105	17954	140	N.S.	**	**	100
	C	5610	100					18002	128				
	S	5820	118				104	18772	160				104
Head	L	986	19	N.S.	N.S.	N.S.	98	2223	44	N.S.	N.S.	N.S.	105
	C	1002	19					2127	38				
	S	1023	22				102	2223	49				105
Feet	L	414	12	N.S.	**	N.S.	108	820	11	**	**	**	107
	C	382	12					766	10				
	S	355	12				93	713	11				93
Pelt	L	1365	70	N.S.	N.S.	N.S.	95	4383	118	N.S.	**	N.S.	96
	C	1431	74					4563	110				
	S	1366	80				95	4863	132				107
Heart	L	77	6	N.S.	N.S.	N.S.	89	173	3	N.S.	N.S.	N.S.	104
	C	87	7					167	3				
	S	96	9				110	173	4				103
Total thoracic organs	L	321	15	N.S.	N.S.	N.S.	99	774	19	N.S.	N.S.	N.S.	100
	C	323	15					779	18				
	S	315	17				98	782	21				100
Liver	L	283	16	N.S.	N.S.	N.S.	98	619	14	N.S.	*	N.S.	95
	C	290	17					650	14				
	S	327	21				113	668	16				103
Kidneys	L	49	3	N.S.	N.S.	N.S.	96	96	2	N.S.	N.S.	N.S.	103
	C	51	4					93	2				
	S	54	4				106	93	2				100
Alimentary tract	L	959	50	*	N.S.	N.S.	85	2329	65	N.S.	N.S.	N.S.	101
	C	1122	58					2312	60				
	S	1096	65				98	2306	71				100
Intestinal fat	L							837	56	**	**	N.S.	79
	C							1061	65				
	S							1070	78				101
Kidney fat	L	59	6	N.S.	*	N.S.	87	449	26	**	N.S.	*	84
	C	68	7					535	28				
	S	81	9				119	454	28				85
Dressing %	L							47.99	0.48	N.S.	*	N.S.	99
	C							48.23	0.44				
	S							49.20	0.53				102

+) Adjusted for daily D.M. intake

Table A.8.2. Iceland.

Component	Type	PFEB = 15.0 kg Mean (g)	SE	Significic. level	Relative difference (short=100)	PFEB = 30.0 kg Mean (g)	SE	Significic. level	Relative difference (short=100)
Carcass	Long	8783	119.7	N.S.	97	17601	181.5	**	96
	Short	9056	120.1		-	18316	197.3		-
Head	Long	1065	10.9	*	103	1832	37.4	*	107
	Short	1032	10.3		-	1716	36.6		-
Feet	Long	503.7	5.9	***	118	714.7	7.7	***	118
	Short	428.2	4.9		-	606.8	6.9		-
Pelt	Long	1604	38.7	N.S.	103	3720	105.9	N.S.	103
	Short	1562	36.7		-	3608	107.3		-
Blood	Long	835	18.3	*	108	1542	37.9	**	111
	Short	774	16.5		-	1392	35.7		-
Tot. thoracic organs	Long	558.6	11.9	***	117	943.0	23.2	**	112
	Short	477.5	9.9		-	840.9	21.6		-
Tot. alimentary tract	Long	1531.8	39.7	N.S.	107	2554.9	65.1	*	108
	Short	1437.4	36.3		-	2374.8	63.2		-
Liver	Long	335.0	6.6	N.S.	102	685.3	20.4	N.S.	99
	Short	329.7	6.3		-	690.2	21.5		-
Spleen	Long	28.7	1.4	N.S.	110	42.8	1.3	N.S.	105
	Short	26.1	1.2		-	40.9	1.3		-
Pancreas	Long	24.6	1.2	N.S.	97	55.4	2.1	*	114
	Short	25.3	1.2		-	48.7	1.9		-
Thyroid	Long	1.75	0.13	**	135	3.80	0.41	N.S.	109
	Short	1.30	0.13		-	3.49	0.43		-
Neck thymus	Long	29.7	3.6	*	146	28.3	4.1	N.S.	140
	Short	20.4	2.4		-	20.2	3.1		-
Heart thymus	Long	25.5	3.2	***	207	27.6	2.7	N.S.	87
	Short	12.3	1.5		-	31.6	3.2		-
Pericardium + bloodvessels + fat	Long	49.9	3.6	N.S.	96	123.8	8.4	N.S.	93
	Short	51.8	3.6		-	133.3	9.5		-
Heart	Long	108.1	2.4	**	111	189.6	4.2	*	108
	Short	97.1	2.1		-	176.1	4.1		-
Lungs + trachea	Long	247.3	6.7	***	120	389.3	11.5	***	130
	Short	205.5	5.4		-	300.1	9.3		-
Diaphragm	Long	84.9	1.8	**	108	171.5	3.5	N.S.	106
	Short	78.4	1.6		-	162.4	3.5		-
Kidneys	Long	66.8	1.7	N.S.	106	102.8	2.3	N.S.	101
	Short	63.3	1.5		-	101.9	2.4		-

Table A.8.2. Iceland. (continued)

Component	Type	PFEB = 15.0 kg Mean (g)	SE	Significic. level	Relative difference (short=100)	PFEB = 30.0 kg Mean (g)	SE	Significic. level	Relative difference (short=100)
Gall bladder	Long	1.17	0.12	N.S.	105	2.84	0.20	N.S.	94
	Short	1.11	0.11		-	3.01	0.22		-
Urine bladder	Long	6.3	0.3	N.S.	113	11.7	0.9	N.S.	101
	Short	5.6	0.2		-	11.6	0.9		-
Penis +	Long	24.7	2.0	N.S.	98	55.5	3.2	*	122
	Short	25.1	2.0		-	45.6	2.7		-
Testicles	Long	42.5	8.3	N.S.	94	284.8	24.6	N.S.	103
	Short	45.4	8.7		-	277.7	25.4		-
Uterus + vagina	Long	15.7	1.3	N.S.	125	31.1	2.1	***	188
	Short	12.6	1.0		-	16.5	1.2		-
Ovaries	Long	0.90	0.18	N.S.	103	1.73	0.18	N.S.	116
	Short	0.87	0.17		-	1.49	0.16		-
Oesophagus	Long	29.0	1.1	N.S.	107	55.2	5.4	*	140
	Short	27.2	1.1		-	39.3	4.0		-
Rumen	Long	304.2	9.0	N.S.	100	798.3	25.7	N.S.	98
	Short	303.3	8.8		-	810.7	27.2		-
Reticulum	Long	50.3	1.6	**	114	113.3	2.8	**	111
	Short	44.0	1.4		-	102.3	2.6		-
Omasum	Long	29.4	1.8	**	127	70.9	4.4	**	127
	Short	23.2	1.4		-	55.8	3.6		-
Abomasum	Long	103.2	5.4	N.S.	102	167.9	6.7	N.S.	104
	Short	101.1	5.1		-	160.7	6.7		-
Small intestine	Long	716.1	25.8	*	112	819.1	26.4	***	118
	Short	636.9	22.3		-	692.0	23.3		-
Caecum	Long	70.6	4.4	N.S.	110	125.4	12.2	N.S.	99
	Short	64.2	3.9		-	126.1	12.8		-
Colon + rectum	Long	194.5	11.7	N.S.	100	380.1	28.4	N.S.	110
	Short	194.3	11.3		-	346.6	27.0		-
Caul fat	Long	169	19.2	**	65	1219	74.8	*	83
	Short	260	28.7		-	1466	94.1		-
Mesenteric fat	Long	187	6.8	N.S.	100	529	24.5	*	87
	Short	188	6.7		-	605	29.3		-
Kidney fat	Long	126	11.5	***	60	730	38.3	***	68
	Short	209	18.6		-	1078	59.0		-
Cannel fat	Long	22	2.2	**	68	90	8.4	N.S.	99
	Short	33	3.1		-	91	8.9		-

APPENDIX 9.

LINEAR CARCASS MEASUREMENTS.

(Estimated by log-log regressions at 16.0 kg carcass weight).

Table A.9.1. Edinburgh.

Measurement	Line	Mean (mm)	SE	Significance level L-C	L-S	C-S	Relat. diff. (C = 100)
Leg length (T)	L	220	3.3				106
	C	207	3.2	**	**	**	
	S	198	3.3				96
Depth of crutch (F)	L	276	6.4				111
	C	249	5.9	**	**	**	
	S	236	6.1				95
Width of gigots (G)	L	231	4.9				100
	C	230	4.9	N.S.	N.S.	N.S.	
	S	227	5.3				99
Width of thorax (V)	L	171	2.2				101
	C	169	2.2	N.S.	N.S.	N.S.	
	S	167	2.4				99
Depth of thorax (Th)	L	260	2.0				101
	C	256	2.0	*	**	**	
	S	250	2.2				98
Carcass length (L)	L	589	6.0				101
	C	586	5.9	N.S.	N.S.	N.S.	
	S	583	6.6				99
F - T	L	56	3.6				133
	C	42	3.4	**	**	N.S.	
	S	38	3.5				90
L. dorsi length (A)	L	54.7	1.5				103
	C	53.0	1.5	N.S.	N.S.	N.S.	
	S	54.1	1.6				102
L. dorsi depth (B)	L	24.9	0.8				91
	C	27.4	0.8	*	*	N.S.	
	S	27.5	0.9				100
Fat over L. dorsi (C)	L	3.6	0.3				90
	C	4.0	0.4	N.S.	N.S.	N.S.	
	S	3.8	0.4				95
Fat on side (J)	L	8.7	0.7				92
	C	9.5	0.8	N.S.	N.S.	N.S.	
	S	9.0	0.9				95
A x B	L	1362	-				94
	C	1452	-	-	-	-	
	S	1488	-				102

Table A.9.2. Iceland.

Measurement	Conf. type	Mean (mm)	SE	Significance level	Relative difference (short=100)
T	Long	211	1.3	***	113
	Short	188	1.2		-
F	Long	283	2.6	***	119
	Short	238	2.2		-
G	Long	231	1.7	*	98
	Short	236	1.7		-
TH	Long	272	1.4	***	108
	Short	252	1.3		-
V	Long	167	1.4	***	92
	Short	181	1.6		-
W	Long	172	1.1	***	94
	Short	184	1.2		-
F - T	Long	71	1.8	***	142
	Short	50	1.3		-
V/TH	Long	0.614	0.006	***	86
	Short	0.718	0.006		-
L	Long	595	3.2	***	107
	Short	558	3.1		-
A	Long	52.5	0.5	**	103
	Short	50.8	0.5		-
B	Long	23.0	0.5	***	86
	Short	26.7	0.6		-
C	Long	2.7	0.3	**	69
	Short	3.9	0.4		-
J	Long	6.5	0.4	***	64
	Short	10.2	0.6		-
B/A	Long	0.438	0.008	***	83
	Short	0.525	0.008		-
A x B	Long	1206	32.2	***	89
	Short	1353	36.8		-

APPENDIX 10.

RELATIVE WEIGHT INCREASES OF MUSCLE GROUPS AND INDIVIDUAL MUSCLES OVER THREE AGE INTERVALS.

(Expressed as: Wt. at 16 wks/Wt. at birth etc.)

	Muscle/group	Age interval		
		0-16 wks.	16-74 wks.	0-74 wks.
1	Hind limb - prox. part	7.08	2.25	15.98
2	Hind limb - dist. part	5.19	1.99	10.33
3	Around spinal column	7.52	2.24	16.81
4	Abdominal muscles	12.44	2.29	28.43
5	Fore limb - prox. part	5.90	2.47	14.56
6	Fore limb - dist. part	4.16	2.21	9.19
7	M. joining fore limb to neck	6.40	3.00	19.20
8	M. joining fore limb to thorax	6.20	2.63	16.31
9	M. of neck and thorax	5.32	2.83	15.06
Gr.1:	Tensor fasciae latae	7.19	2.30	16.50
	Biceps femoris	6.86	2.20	15.09
	Gluteus medius	7.54	2.38	17.95
	Semitendinosus	7.22	2.49	18.01
	Quadriceps femoris	6.53	2.17	14.15
	Gluteus accessorius	6.18	2.30	14.24
	Gluteus profundus	5.87	2.14	12.57
	Gemellus	4.49	2.04	9.16
	Quadratus femoris	5.06	2.36	11.93
	Gracilis	7.39	2.22	16.43
	Sartorius	5.51	2.07	11.43
	Pectineus	7.43	2.09	15.54
	Semimembranosus	8.08	2.28	18.46
	Adductor femoris	7.73	2.18	16.84
	Oburators	7.14	2.38	17.01
Gr.2:	Gastrocnemius	5.64	1.86	10.49
	Soleus	3.03	1.54	4.66
	Ext. digit. lateralis	3.99	1.72	6.86
	Peroneus longus	4.79	2.01	9.64
	Peroneus tertius	4.34	2.33	10.11
	Tibialis anterior	4.64	1.95	9.04
	Flexor group	5.46	2.16	11.79

(Continued)	Age interval		
	0-16 wks.	16-74 wks.	0-74 wks.
Gr.3: Iliacus	6.66	2.11	14.07
Psoas major	8.05	2.14	17.18
Psoas minor	7.09	2.00	14.16
Quadratus lumborum	4.99	2.26	11.25
Longissimus dorsi	8.45	2.16	18.26
Multifidus dorsi	5.92	2.60	15.36
Gr.4: Panniculus carnosus	12.81	2.31	29.61
Serrat. dors. caudalis	6.05	2.45	14.85
Obliq. abd.ext.	11.00	2.29	25.22
Rectus abdominis	11.34	2.21	25.04
Obliq. abd. int.	18.16	2.41	43.70
Transversus abdominis	13.55	2.23	30.24
Gr.5: Deltoideus	5.84	2.79	16.32
Tensor fasciae antibr.	6.50	2.99	19.45
Infraspinatus	6.75	2.75	18.55
Teres minor	4.92	2.82	13.87
Supraspinatus	6.15	2.36	14.50
Subscapularis	6.07	2.55	15.52
Coracobrachialis	5.02	2.42	12.14
Teres major	6.16	2.76	17.01
Triceps brachii	5.67	2.30	13.03
Biceps brachii	5.55	2.37	13.17
Brachialis	4.23	2.19	9.27
Gr.6: Flexor group	4.50	2.23	10.03
Extensor group	3.71	2.18	8.09
Gr.7: Trapezius cervicalis	4.62	3.07	14.21
Brachiocephalicus	4.94	2.90	14.33
Omotransversarius	3.81	3.63	13.80
Serratus ventralis	7.81	2.96	23.11
Gr.8: Latissimus dorsi	6.02	2.66	16.00
Pectoral. prof. + superfic.	6.23	2.59	16.10
Rhomboideus	6.42	2.82	18.14
Gr.9: Scalenus dorsalis	6.35	2.88	18.32
Sternocephalicus	6.28	3.47	21.77
Splenius	4.81	5.94	28.61

(Continued)	Age interval		
	0-16 wks.	16-74 wks.	0-74 wks.
Gr.9: Scal. ventralis	5.31	3.45	18.35
Long. cap. et atlantis	4.32	4.67	20.17
Complexus	4.39	2.82	12.39
Rect. cap. dors. major	4.00	2.80	11.20
Obl. cap. posterior	5.92	2.60	15.39
Serr. dors. cranialis	5.40	3.76	20.25
Transversus thoracic	5.34	2.10	11.22
Longissimus costarum	6.18	2.98	18.43
Longus colli	5.77	2.25	12.96
Intravers. colli	5.61	2.69	15.09
Multifidus cervicis	5.28	2.57	13.60
Intercostales	5.43	2.60	14.14

APPENDIX 11.

RELATIVE GROWTH COEFFICIENTS RELATING INDIVIDUAL MUSCLE WEIGHTS TO THE WEIGHT OF TOTAL CARCASS MUSCLE.

Table A.11.1. Edinburgh.

Muscle	Pre-trial[+] (12-19 wks.) b	SE	On trial[++] (19-48 wks.) b	SE	Signific. of diff.	+++ Classifi-cation
Group 1:						
Gluteus medius	1.03	0.072	1.04	0.039	N.S.	A
Semimenbranosus	0.79	0.048	1.03	0.043	**	VL-A
Semitendinosus	0.95	0.090	1.10	0.052	N.S.	L-H
Quadriceps femoris	1.00	0.050	0.88	0.030	*	A-L
Group 2:						
Gastrocnemius	0.99	0.071	0.84	0.069	N.S.	A-L
Extensor digitorum longus	1.14	0.219	0.61	0.089	*	H-VL
Group 3:						
Longissimus dorsi	1.08	0.046	1.11	0.050	N.S.	H
" in shoulder	0.66	0.087	0.94	0.094	*	VL-L
" in rib	0.97	0.067	0.97	0.145	N.S.	A
" in loin	1.22	0.082	1.16	0.060	N.S.	VH-H
Psoas major (in loin)	1.05	0.106	1.06	0.068	N.S.	(H)
Psoas minor (in loin)	0.97	0.202	0.85	0.117	N.S.	A-L
Group 5:						
Infraspinatus	1.14	0.081	1.03	0.040	N.S.	H-A
Supraspinatus	0.80	0.068	0.96	0.040	*	L-A
Biceps brachii	0.80	0.078	0.90	0.050	N.S.	L
Brachialis	0.78	0.117	0.73	0.070	N.S.	VL
Group 6:						
Extensor carpi radialis	0.87	0.119	0.60	0.073	N.S.	L-VL

+) Individual muscles were not dissected from the birth group.

++) Adjusted to constant daily D.M. intake.

+++) Classification into very high (VH), high (H), average (A) low (L) and very low (VL) refers to relative growth coefficients:

VH: $b > 1.20$

H: $1.05 \leq b \leq 1.20$

A: $0.95 < b < 1.05$

L: $0.80 \leq b \leq 0.95$

VL: $b < 0.80$

Table A.11.2. Iceland.[+]

a) All muscles: Birth-16 wks. and 16-74 wks.

Muscle	Age: 0-16 wks. b	SE	Age: 16-74 wks. b	SE	Signific. of diff.	Classification[+]
Group 1:						
Tensor fasciae latae	1.03	0.018	0.98	0.042	N.S.	A
Biceps femoris [x]	1.03	0.012	0.98	0.028	N.S.	H-A
Gluteus medius	1.08	0.019	1.07	0.033	N.S.	H
Semitendinosus	1.04	0.013	1.06	0.029	N.S.	A
Quadriceps femoris	0.99	0.012	0.90	0.024	*	A-L
Gluteus accessorius	1.00	0.041	1.03	0.048	N.S.	A
Gluteus profundus	0.93	0.044	0.86	0.051	N.S.	L
Gemellus	0.78	0.034	0.76	0.075	N.S.	VL
Quadratus femoris	0.84	0.044	0.82	0.089	N.S.	L
Gracilis	1.05	0.015	0.97	0.035	N.S.	H-(A)
Sartorius	0.89	0.051	0.98	0.082	N.S.	(L-A)
Pectineus	1.06	0.020	0.87	0.035	**	H-L
Semimembranosus	1.10	0.019	0.97	0.026	**	H-A
Adductor femoris	1.08	0.015	0.91	0.026	***	H-L
Oburators	1.02	0.029	0.97	0.052	N.S.	A
Group 2:						
Gastrocnemius	0.92	0.023	0.78	0.032	*	L-VL
Soleus	0.59	0.066	0.68	0.123	N.S.	VL
Extensor digit. lateralis	0.73	0.040	0.69	0.059	N.S.	VL
Peroneus longus	0.83	0.024	0.87	0.054	N.S.	L
Peroneus tertius (+long ext.gr.)	0.78	0.017	0.97	0.031	**	VL-A
Tibialis anterior	0.80	0.028	0.80	0.051	N.S.	L
Flexor group	0.89	0.017	0.90	0.033	N.S.	L
Group 3:						
Iliacus	0.98	0.020	0.92	0.047	N.S.	A-(L)
Psoas major [x]	1.10	0.016	0.92	0.030	**	H-(A)-L
Psoas minor	1.01	0.095	1.03	0.127	N.S.	A
Quadratus lumborum	0.85	0.035	0.91	0.043	N.S.	L
Longissimus dorsi [x]	1.13	0.014	0.91	0.028	***	H-A-L
Multifidus dorsi	0.94	0.016	1.03	0.035	N.S.	L-(A)
Group 4:						
Panniculus carnosus	1.38	0.027	0.98	0.045	***	VH-A
Serratus dorsalis caudalis	0.97	0.045	0.98	0.087	N.S.	A

Table A.11.2.a. (continued)

Muscle	Age: 0-16 wks. b	SE	Age: 16-74 wks. b	SE	Signific. of diff.	+ Classification
Group 4:						
Obliqus abdom. externus	1.24	0.029	0.93	0.043	***	VH-L
Rectus abdominis	1.26	0.020	0.93	0.035	***	VH-L
Obliqus abdom. internus	1.50	0.024	0.98	0.040	***	VH-A
Transversus abdominis	1.37	0.027	0.84	0.040	***	VH-L
Group 5:						
Deltoideus	0.93	0.022	1.16	0.041	**	L-H
Tensor fasciae antibrachii	1.00	0.099	1.25	0.056	N.S.	A-(VH)
Infraspinatus x	0.99	0.043	1.09	0.033	N.S.	A-VH
Teres minor	0.85	0.019	1.10	0.047	**	L-H
Supraspinatus x	0.95	0.011	0.95	0.031	N.S.	L-H
Subscapularis x	0.96	0.026	1.05	0.032	N.S.	A-H
Coracobrachialis	0.86	0.033	0.98	0.055	N.S.	L-(A)
Teres major	0.97	0.017	1.08	0.057	N.S.	A-(H)
Triceps brachii x	0.92	0.008	0.94	0.019	N.S.	L-(H)
Biceps brachii	0.89	0.023	0.99	0.037	N.S.	L-(A)
Brachialis	0.76	0.021	0.84	0.038	N.S.	VL-(L)
Group 6:						
Flexor group	0.79	0.011	0.90	0.035	*	VL-L
Extensor group	0.70	0.018	0.92	0.034	*	VL-L
Group 7:						
Trapezius cervicalis	0.82	0.019	1.19	0.041	***	L-H
Brachiocephalicus	0.87	0.023	1.19	0.042	***	L-H
Omotransversarius	0.70	0.036	1.28	0.070	***	VL-VH
Serratus ventralis x	1.09	0.014	1.17	0.032	N.S.	H-A-H
Group 8:						
Latissimus dorsi	0.96	0.014	1.11	0.033	**	A-H
Pectoralis profundus + superf. x	0.97	0.015	1.12	0.030	**	A-L-H
Rhomboideus	0.99	0.026	1.16	0.047	*	A-H
Group 9:						
Scalenus dorsalis	0.98	0.098	1.39	0.174	N.S.	A-VH
Sternocephalicus + Sternothyrohyoideus x	0.94	0.034	1.32	0.072	**	L-VH
Splenius x	0.81	0.045	1.63	0.078	***	L-VH-H

Table A.11.2.a. (continued)

Muscle	Age: 0-16 wks. b	SE	Age: 16-74 wks. b	SE	Signific. of diff.	+) Classification
Group 9:						
Scalenus ventr. + Rectus cap. ventralis + Omo-hyoideus	0.88	0.025	1.22	0.049	***	L-VH
Longissim.cap.et atlantis x	0.76	0.056	1.39	0.074	***	VL-VH
Complexus x	0.78	0.018	1.17	0.038	***	VL-A-H
Rectus cap. dors. major	0.73	0.048	0.97	0.066	*	VL-A
Obliqus cap. posterior	0.90	0.040	1.04	0.044	N.S.	L-A
Serratus dors. cranialis	0.77	0.100	1.34	0.181	*	VL-VH
Transversus thoracic	0.90	0.047	0.90	0.080	N.S.	L
Longissimus costarum	0.96	0.032	1.08	0.059	N.S.	A-H
Longus colli	0.91	0.023	0.91	0.046	N.S.	L
Intraversales colli	0.89	0.030	1.08	0.050	*	L-H
Multifidus cervicis	0.87	0.024	0.91	0.071	N.S.	L
Intercostales	0.91	0.010	1.04	0.030	**	L-A

+) Classification into very high (VH), high (H), average (A), low (L) and very low (VL) refers to relative growth coefficients:

VH - $b > 1.20$

H - $1.05 \leq b \leq 1.20$

A - $0.95 < b < 1.05$

L - $0.80 \leq b \leq 0.95$

VL - $b < 0.80$

x) See table A.11.2.b.

Table A.11.2.b. Muscles, whose growth phases were partitioned at other points than 16 weeks.

Muscle	Age interval	b	SE	Classification
Group 1:				
Biceps femoris	Birth- 6 wks.	1.07 [a]	0.016	H-A
	6-74 -	0.96 [b]	0.028	
Group 3:				
Longissimus dorsi	Birth- 6 wks.	1.19 [a]	0.011	
	6-24 -	1.04 [b]	0.040	H-A-L
	48-74 -	0.83 [c]	0.088	
Psoas major	Birth- 6 wks.	1.15 [a]	0.027	
	6-16 -	0.97 [b]	0.045	H-(A)-L
	16-74 -	0.92 [b]	0.030	
Group 4:				
Obliqus absominis externus	Birth- 6 wks.	1.15 [a]	0.040	
	6-16 -	1.47 [b]	0.089	H-VH-L
	16-74 -	0.93 [c]	0.043	
Group 5:				
Infraspinatus	Birth-24 wks.	0.99 [a]	0.043	A-VH
	48-74 -	1.55 [b]	0.158	
Supraspinatus	Birth-24 wks.	0.90 [a]	0.011	L-H
	48-74 -	1.17 [b]	0.120	
Subscapularis	Birth-24 wks.	0.96 [a]	0.026	A-(V)H
	48-74 -	1.23 [b]	0.126	
Triceps brachii	Birth-24 wks.	0.91	0.008	A
	48-74 -	1.07	0.102	(L-H)
Group 6:				
Flexor group	Birth-24 wks.	0.76	0.011	L
	48-74 -	0.92	0.139	(VL-L)
Group 7:				
Serratus ventralis	Birth- 6 wks.	1.13 [a]	0.019	
	6-16 -	0.99 [b]	0.047	H-A-H
	16-74 -	1.17 [a]	0.032	

Table A.11.2.b. (continued)

Muscle	Age interval	b	SE	Classification
Group 8:				
Pectoralis profundus	Birth- 6 wks.	1.01 [a]	0.021	
+ superficialis	6-16 -	0.86 [b]	0.045	A-L-H
	16-74	1.12 [c]	0.030	
Group 9: .				
Sternocephalicus	Birth- 6 wks.	0.83 [a]	0.051	
+ sternothyrohyoideus	6-16 -	1.24 [b]	0.109	L-VH
	16-74	1.32 [b]	0.072	
Splenius	Birth-16 wks.	0.81 [a]	0.045	
	16-24 -	1.78 [b]	0.161	L-VH-H
	48-74 -	1.12 [a]	0.141	
Longissimus capitis	Birth- 6 wks.	0.56 [a]	0.093	
et atlantis	6-16 -	1.21 [b]	0.113	VL-VH
	16-74 -	1.39 [b]	0.074	
Complexus	Birth- 6 wks.	0.72 [a]	0.022	
	6-16 -	0.96 [b]	0.054	VL-A-H
	16-74 -	1.17 [c]	0.038	

+) All coefficients adjusted for conformation type, sex and type of birth.

APPENDIX 12.

MEAN WEIGHTS OF MUSCLE GROUPS AND INDIVIDUAL MUSCLES ESTIMATED BY REGRESSIONS AT 2.5 Kg AND 5.0 Kg HALF-CARCASS MUSCLE WEIGHTS.

(Effects of sex and type of birth have been removed.) Iceland.

Muscle group	Type	Side-muscle wt. = 2500 g				Side-muscle wt. = 5000 g			
		Mean (g)	SE	Signific. level	Relative diff. (short=100)	Mean (g)	SE	Signific. level	Relative diff. (short=100)
1. Hind limb-proximal part	Long	713.8	5.1	N.S.	100	1391.6	8.6	N.S.	100
	Short	709.9	5.3		-	1388.1	9.0		-
2. Hind limb-distal part	Long	138.4	2.3	N.S.	99	244.6	2.6	N.S.	100
	Short	140.4	2.4		-	245.4	2.7		-
3. Around spinal column	Long	367.0	4.0	***	94	751.1	9.2	*	96
	Short	389.4	4.4		-	783.8	11.0		-
4. Abdominal muscles	Long	231.2	5.0	*	92	511.8	5.4	***	90
	Short	251.2	5.6		-	569.6	6.2		-
5. Fore limb-proximal part	Long	327.1	3.2	***	106	615.8	6.3	***	106
	Short	307.7	3.1		-	581.4	6.9		-
6. Fore limb-distal part	Long	87.3	1.1	N.S.	103	153.6	1.4	***	104
	Short	84.8	1.1		-	147.0	1.4		-
7. Muscles joining fore limb to neck	Long	190.1	2.8	**	106	406.0	4.2	***	105
	Short	179.5	2.7		-	385.7	4.2		-
8. Muscles joining fore limb to thorax	Long	161.6	2.5	N.S.	100	333.3	3.4	N.S.	99
	Short	161.4	2.6		-	336.5	3.6		-
9. Muscles of neck and thorax	Long	274.5	2.9	*	103	587.8	5.8	***	106
	Short	266.0	2.9		-	555.0	5.7		-
Tensor fasciae latae (1)	Long	25.3	0.6	N.S.	96	53.4	1.0	N.S.	103
	Short	26.4	0.6		-	51.8	1.0		-
Biceps femoris (1)	Long	122.5	1.7	N.S.	99	236.1	2.8	N.S.	99
	Short	123.3	1.8		-	238.6	3.0		-
Gluteus medius (1)	Long	73.2	1.7	N.S.	99	151.3	2.2	N.S.	99
	Short	74.0	1.7		-	152.8	2.3		-
Semitendinosus (1)	Long	45.2	0.7	***	112	92.6	1.2	***	108
	Short	40.5	0.7		-	85.4	1.1		-
Quadriceps femoris (1)	Long	190.5	2.7	N.S.	100	354.4	3.7	N.S.	100
	Short	190.0	2.8		-	354.5	3.9		-
Gluteus accessorius (1)	Long	13.2	0.6	N.S.	112	25.0	0.5	**	109
	Short	11.8	0.6		-	22.9	0.5		-
Gluteus profundus (1)	Long	8.9	0.5	N.S.	111	16.4	0.4	**	110
	Short	8.0	0.4		-	14.9	0.3		-
Gemellus (1)	Long	1.7	0.1	*	121	2.9	0.1	**	116
	Short	1.4	0.1		-	2.5	0.1		-

APPENDIX 12. (continued)

Muscle	Type	Side-muscle wt. = 2500 g				Side muscle wt. = 5000 g			
		Mean (g)	SE	Signific. level	Relative diff. (short=100)	Mean (g)	SE	Signific. level	Reltive diff. (short=100)
Quadratus femoris (1)	Long	2.1	0.1	N.S.	105	4.0	0.2	N.S.	108
	Short	2.0	0.1		-	3.7	0.1		-
Gracilis (1)	Long	25.2	0.5	N.S.	100	49.6	0.8	N.S.	100
	Short	25.3	0.5		-	49.6	0.8		-
Sartorius (1)	Long	4.9	0.3	N.S.	107	8.7	0.3	N.S.	97
	Short	4.6	0.3		-	9.0	0.3		-
Pectineus (1)	Long	15.3	0.4	*	109	28.2	0.4	N.S.	99
	Short	14.1	0.4		-	28.6	0.5		-
Semimembranosus (1)	Long	113.8	2.6	N.S.	95	230.0	2.6	N.S.	97
	Short	119.7	2.8		-	237.0	2.8		-
Adductor femoris (1)	Long	54.0	1.0	N.S.	103	102.8	1.2	N.S.	99
	Short	52.6	1.0		-	104.0	1.2		-
Oburators (1)	Long	16.0	0.6	*	112	32.7	0.7	**	110
	Short	14.3	0.5		-	29.8	0.7		-
Gastrocnemius (2)	Long	69.4	1.9	N.S.	96	119.7	1.6	N.S.	97
	Short	72.2	2.0		-	123.3	1.8		-
Soleus (2)	Long	1.0	0.1	N.S.	125	1.5	0.1	***	136
	Short	0.8	0.1		-	1.1	0.1		-
Extensor digitorum lateralis (2)	Long	7.3	0.3	N.S.	101	12.3	0.3	*	108
	Short	7.2	0.4		-	11.4	0.3		-
Peroneus longus (2)	Long	4.7	0.1	**	90	8.4	0.2	N.S.	94
	Short	5.2	0.2		-	8.9	0.2		-
Peroneus tertius (+extensor group)(2)	Long	17.7	0.4	N.S.	102	32.3	0.4	N.S.	99
	Short	17.3	0.4		-	32.6	0.5		-
Tibialis anterior (2)	Long	5.0	0.2	N.S.	104	8.8	0.2	*	106
	Short	4.8	0.2		-	8.3	0.2		-
Flexor group (2)	Long	33.2	0.7	N.S.	103	60.9	0.9	N.S.	103
	Short	32.2	0.7		-	59.3	0.9		-
Iliacus (3)	Long	20.4	0.5	N.S.	107	39.8	0.8	N.S.	106
	Short	19.1	0.5		-	37.7	0.8		-
Psoas major (3)	Short	38.6	0.8	N.S.	98	74.6	1.0	N.S.	97
	Short	39.2	0.8		-	76.6	1.0		-
Psoas minor (3)	Long	15.9	1.8	N.S.	126	27.4	1.5	N.S.	104
	Short	12.6	1.5		-	26.3	1.5		-

APPENDIX 12. (continued).

Muscle	Type	Side-muscle wt. = 2500 g				Side muscle wt. = 5000 g			
		Mean (g)	SE	Signific. level	Relative diff. (short=100)	Mean (g)	SE	Signific. level	Relative diff. (short=100)
Quadratus lumborum (3)	Long	7.9	0.3	N.S.	103	15.0	0.3	*	106
	Short	7.7	0.3		-	14.2	0.3		-
Longissimus dorsi (3)	Long	209.9	3.6	***	90	444.6	8.3	**	93
	Short	232.2	4.2		-	478.6	10.3		-
Multifidus dorsi (3)	Long	73.4	1.4	N.S.	96	149.5	2.2	N.S.	98
	Short	76.4	1.5		-	153.1	2.4		
Panniculus carnosus (4)	Long	51.8	1.7	N.S.	96	117.7	2.3	N.S.	95
	Short	54.2	1.8		-	123.9	2.5		-
Serratus dorsalis caudalis (4)	Long	4.9	0.3	N.S.	89	9.8	0.4	*	89
	Short	5.5	0.3		-	11.0	0.4		-
Obliqus abdominis externus (4)	Long	44.0	1.5	N.S.	94	96.2	1.8	***	88
	Short	46.9	1.7		-	109.0	2.1		-
Rectus absominis (4)	Long	58.3	1.4	N.S.	94	122.9	1.8	***	90
	Short	61.8	1.6		-	136.3	2.1		-
Obliqus abdominis internus (4)	Long	32.3	0.9	**	87	78.0	1.3	***	86
	Short	37.1	1.1		-	90.2	1.6		-
Transversus abdominis (4)	Long	38.4	1.3	**	86	85.0	1.5	***	87
	Short	44.7	1.5		-	97.5	1.8		-
Deltoideus (5)	Long	11.4	0.3	N.S.	94	23.9	0.4	N.S.	98
	Short	12.1	0.3		-	24.3	0.5		-
Tensor fasciae antibrachii (5)	Long	5.9	0.7	N.S.	95	14.4	0.3	*	107
	Short	6.2	0.8		-	13.4	0.3		-
Infraspinatus (5)	Long	50.9	2.6	N.S.	94	109.1	2.3	N.S.	100
	Short	54.0	2.9		-	109.0	2.7		-
Teres minor (5)	Long	4.1	0.1	N.S.	98	8.1	0.2	N.S.	96
	Short	4.2	0.1		-	8.4	0.2		-
Supraspinatus (5)	Long	64.8	0.9	***	116	116.9	2.4	***	116
	Short	55.8	0.8		-	100.9	2.4		-
Subscapularis (5)	Long	29.5	0.7	**	110	54.9	1.3	N.S.	107
	Short	26.7	0.6		-	51.4	1.4		-
Coracobrachialis (5)	Long	4.1	0.2	N.S.	98	7.8	0.2	N.S.	99
	Short	4.2	0.2		-	7.9	0.2		-
Teres major (5)	Long	13.2	0.3	***	113	25.3	0.6	N.S.	100
	Short	11.7	0.2		-	25.3	0.6		-
Triceps brachii (5)	Long	112.1	1.1	***	106	202.5	2.8	N.S.	103
	Short	105.9	1.1		-	195.8	3.1		-

APPENDIX 12. (continued)

Muscle	Type	Side-muscle wt. = 2500 g				Side muscle wt. = 5000 g			
		Mean (g)	SE	Signific. level	(short=100)	Mean (g)	SE	Sifnific. level	Relative diff. (short=100)
Biceps brachii (5)	Long	14.8	0.4	N.S.	103	28.6	0.4	N.S.	102
	Short	14.3	0.4		-	28.1	0.5		-
Brachialis (5)	Long	13.8	0.3	***	118	23.6	0,4	***	116
	Short	11.7	0.3		-	20.3	0.3		-
Flexor group (6)	Long	53.6	0.7	*	105	91.4	2.2	***	115
	Short	51.0	0.7		-	79.8	2.3		-
Extensor group (6)	Long	33.7	0.7	N.S.	100	59.7	0.9	N.S.	100
	Short	33.7	0.8		-	59.7	0.9		-
Trapezius cervicalis (7)	Long	20.0	0.4	N.S.	100	41.6	0.7	N.S.	100
	Short	20.1	0.5		-	41.7	0.8		-
Brachiocephalicus (7)	Long	30.6	0.9	*	108	66.8	1.2	***	109
	Short	28.3	0.8		-	61.5	1.1		-
Omotransversarius (7)	Long	11.3	0.5	N.S.	105	25.2	0.8	N.S.	107
	Short	10.8	0.5		-	23.5	0.7		-
Serratus ventralis (7)	Long	127.3	2.2	*	106	270.8	3.7	*	105
	Short	119.7	2.1		-	257.9	3.7		-
Latissimus dorsi (8)	Long	38.8	0.7	N.S.	97	80.5	1.2	N.S.	97
	Short	40.3	0.7		-	83.0	1.2		-
Pectoralis profundus + superficialis (8)	Long	105.2	1.9	N.S.	102	216.1	2.7	N.S.	99
	Short	103.1	1.9		-	217.2	2.9		-
Rhomboideus (8)	Long	17.4	0.5	N.S.	97	36.3	0.7	N.S.	101
	Short	17.9	0.6		-	35.8	0.8		-
Scalenus dorsalis (9)	Long	1.3	0.2	N.S.	81	2.8	0.2	*	80
	Short	1.6	0.2		-	3.5	0.3		-
Sternocephalicus + Sternothyrohyoideus (9)	Long	15.0	0.6	N.S.	105	38.3	1.2	N.S.	106
	Short	14.3	0.6		-	36.0	1.2		-
Splenius (9)	Long	4.6	0.3	N.S.	102	14.3	0.9	N.S.	111
	Short	4.5	0.3		-	12.9	1.0		-
Scal. ventr. + rect. cap. ventr. + omo-hyoideus (9)	Long	26.8	0.8	N.S.	102	63.1	1.3	N.S.	104
	Short	26.3	0.8		-	60.7	1.3		-
Longissimus capitis et atlantis (9)	Long	5.3	0.4	N.S.	100	13.9	0.4	N.S.	100
	Short	5.3	0.4		-	13.9	0.5		-
Complexus (9)	Long	30.8	0.7	N.S.	99	63.8	1.1	*	106
	Short	31.1	0.7		-	60.0	1.0		-

APPENDIX 12. (continued)

Muscle	Type	Side-muscle wt. = 2500 g. Mean (g)	SE	Significic. level	Relative diff. (short=100)	Side-muscle wt. = 5000 g. Mean (g)	SE	Significic. level	Relative diff. (short=100)
Rectus capitis dorsalis major (9)	Long	3.2	0.2	N.S.	100	6.7	0.2	N.S.	108
	Short	3.2	0.2		-	6.2	0.2		-
Obliqus capitis posterior (9)	Long	12.7	0.6	**	122	25.1	0.5	***	113
	Short	10.4	0.5		-	22.3	0.4		-
Serratus dorsalis cranialis (9)	Long	0.3	0.0	*	60	0.9	0.1	N.S.	90
	Short	0.5	0.1		-	1.0	0.1		-
Transversus thoracis (9)	Long	5.8	0.3	N.S.	100	11.0	0.4	N.S.	103
	Short	5.8	0.3		-	10.7	0.4		-
Longissimus costarum (9)	Long	9.2	0.4	N.S.	100	20.7	0.5	***	115
	Short	9.2	0.4		-	18.0	0.5		-
Longus colli (9)	Long	28.8	0.8	N.S.	107	56.7	1.1	N.S.	105
	Short	27.0	0.8		-	54.1	1.1		-
Intraversales colli (9)	Long	20.1	0.7	N.S.	99	44.6	1.0	N.S.	104
	Short	20.3	0.7		-	43.0	1.0		-
Multifidus cervicis (9)	Long	23.2	0.7	N.S.	103	48.5	1.5	N.S.	109
	Short	22.6	0.7		-	44.5	1.4		-
Intercostales (9)	Long	78.7	1.0	N.S.	103	159.8	2.1	**	106
	Short	76.6	1.0		-	151.1	2.1		-

Values in parentheses refer to constituting muscle groups.

APPENDIX 13.

MUSCLE GROUPS AS PERCENTAGE OF TOTAL CARCASS MUSCLE AT VARYING AGES. (ICELAND) - EFFECT OF SEX. (adjusted for conformation type and type of birth).

Muscle group	Sex	At birth	AGE (weeks) 6	16	24	48	74
Total muscle (wt. in g)	M	1063	4079	7220	9904[a]	14908[a]	18284[a]
	F	914	3865	7071	9247[b]	10800[b]	13401[b]
Gr.1 - Proximal hind limb	M	26.0[a]	28.6[a]	28.0[a]	27.1[a]	26.5[a]	25.4[a]
	F	27.7[b]	28.8[b]	29.3[b]	29.3[b]	28.8[b]	28.3[b]
Gr.2 - Distal hind limb	M	6.9	5.4	5.4	4.9	4.7	4.3
	F	7.1	5.8	5.3	5.1	4.9	4.7
Gr.3 - Around spinal column	M	13.3	15.5	15.0	14.8	14.3[a]	14.1
	F	13.4	15.5	15.4	15.3	15.4[b]	14.0
Gr.4 - Abdominal	M	5.9	8.3	11.2	10.8	11.2	10.3
	F	5.5	8.7	10.6	10.5	10.4	10.8
Gr.5 - Proximal fore limb	M	14.4	13.3	12.3	11.9	11.7	12.9
	F	14.0	12.6	12.7	12.1	12.2	12.8
Gr.6 - Distal fore limb	M	5.2	3.7	3.2	3.0	2.9	3.0
	F	5.2	3.7	3.1	2.9	3.1	2.9
Gr.7 - Joining fore limb to neck	M	7.9	7.6	7.4	8.1	8.2[a]	9.4[a]
	F	7.3	7.5	7.2	7.7	7.4[b]	8.6[b]
Gr.8 - Joining fore limb to thorax	M	7.1[a]	6.6	6.2	6.8	7.2	6.6
	F	6.4[b]	6.9	6.3	6.8	6.8	7.3
Gr.9 - Intrinsic of neck and thorax	M	13.4	11.1	11.2[a]	12.6[a]	13.2[a]	14.0[a]
	F	13.5	10.4	10.0[b]	10.4[b]	10.9[b]	10.5[b]

APPENDIX 14.

RELATIVE GROWTH OF INDIVIDUAL VERTEBRAE AND RIBS. (ICELAND).

- Adjusted for conformation type, sex and type of birth.

Table A.14.1. VERTEBRAE - related to total spinal column weight.

Bone	Age: 0-74 wks.		Age:16-74 wks.		Signific. of diff.
	b	SE	b	SE	
Total cervical	1.00	0.015	1.11	0.015	**
Cervical 1	1.02	0.022	1.04	0.026	N.S.
- 2	0.97	0.017	1.00	0.018	N.S.
- 3	1.00	0.022	1.23	0.018	***
- 4	1.05	0.017	1.18	0.020	**
- 5	1.02	0.018	1.12	0.023	*
- 6	1.01	0.016	1.11	0.028	*
- 7	0.94	0.015	1.09	0.022	**
Total thoracic	0.97	0.012	0.97	0.016	N.S.
Thoracic 1	0.94	0.019	0.98	0.017	N.S
- 2	0.95	0.016	0.99	0.024	N.S.
- 3	1.00	0.016	1.05	0.020	N.S.
- 4	1.02	0.014	1.00	0.022	N.S.
- 5	1.03	0.019	1.03	0.029	N.S.
- 6	0.98	0.015	0.99	0.021	N.S.
- 7	0.96	0.014	0.96	0.021	N.S.
- 8	0.95	0.018	0.93	0.022	N.S.
- 9	0.97	0.014	0.90	0.018	*
- 10	0.97	0.014	0.91	0.020	N.S.
- 11	0.95	0.018	0.90	0.023	N.S.
- 12	0.98	0.026	0.92	0.026	N.S.
- 13	1.00	0.025	0.92	0.027	N.S.
Total lumbar	1.02	0.016	0.89	0.022	**
Lumbar 1	1.00	0.019	0.93	0.025	N.S.
- 2	1.03	0.016	0.91	0.020	**
- 3	1.01	0.011	0.91	0.017	*
- 4	1.02	0.014	0.91	0.017	**
- 5	1.01	0.013	0.90	0.019	**
- 6	1.00	0.015	0.92	0.028	N.S.
Sacral + coccygeal	1.02	0.037	0.98	0.039	N.S.

Table A.14.2. RIBS - Related to total rib weight.

Bone		Age: 0-16 wks.		Age:16-74 wks.		Sifnific. of diff.
		b	SE	b	SE	
Rib	1	0.84	0.039	1.14	0.045	**
-	2	0.90	0.017	0.97	0.030	N.S.
-	3	0.96	0.015	0.96	0.025	N.S.
-	4	0.98	0.014	0.96	0.021	N.S.
-	5	0.99	0.017	0.93	0.021	N.S.
-	6	1.04	0.015	0.91	0.025	**
-	7	1.08	0.016	0.90	0.026	**
-	8	1.02	0.019	0.91	0.028	*
-	9	0.99	0.024	1.02	0.027	N.S.
-	10	1.03	0.020	1.10	0.029	N.S.
-	11	1.07	0.019	1.17	0.031	*
-	12	1.10	0.024	1.23	0.037	*
-	13	1.13	0.027	1.28	0.038	*